# ABSTRACT

Title of thesis: ECOLOGY OF JUVENILE BLUEFISH, *POMATOMUS SALTATRIX*, IN MARYLAND COASTAL WATERS AND CHESAPEAKE BAY

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Shallow coastal ocean environments may function as important nursery habitats for juvenile bluefish, yet little ecological research has been conducted in ocean habitats. This thesis examines seasonal production, growth rates, and diet composition of juveniles in Maryland's coastal ocean environment and the Chesapeake Bay estuary. Summer-spawned juveniles dominated in ocean habitats and exhibited rapid growth rates, 2.0 – 2.4 mm $d^{-1}$, which were likely fueled by an abundant forage base of young-of-the-year bay anchovy present in ocean environments during late summer/early fall. This summer cohort was rare in the Chesapeake Bay, where spring-spawned juveniles dominated. These results suggest ocean habitats provide principal nurseries for summer-spawned bluefish, and that the Chesapeake Bay and other estuaries are principal nurseries for spring-spawned juveniles. Accordingly, year class strength is likely shaped by contributions of juveniles from both oceanic and estuarine nursery habitats.

# ECOLOGY OF JUVENILE BLUEFISH, *POMATOMUS SALTATRIX*, IN MARYLAND COASTAL WATERS AND CHESAPEAKE BAY

by

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# BACKGROUND

Bluefish, *Pomatomus saltatrix*, is a recreationally and economically important species along the Atlantic coast of the United States. A decline of recreational landings, spawning stock biomass, and fishery independent recruitment indices has occurred since the mid 1980s, raising concern over the status of the stock and providing impetus for research investigating possible reasons for the perceived decline of the Western Atlantic bluefish population (ASMFC 2002). Overfishing, an offshore shift of the adult population, changing oceanographic (climate) conditions influencing larval transport/survival, and a decline of suitable nursery habitats for juveniles have all been put forth as potential reasons for the decline of stock abundance and recruitment (Fahay et al. 1999). Of particular relevance to this study is the role of nursery habitats in sustaining juvenile bluefish production. Most recruitment variability of marine fishes is thought to be generated during the larval stage. However, dynamics during the juvenile stage, by dint of relatively long stage duration, are also important in influencing (regulating v. controlling) recruitment levels. For instance, abiotic (e.g., temperature) and biotic (e.g., predator-prey interactions) factors influencing growth and survival of juvenile marine fishes during residency in nursery habitats play a role in shaping year class strength.

Juvenile bluefish are assumed to be estuarine dependent, relying exclusively on estuaries for nursery habitat (McHugh 1967; Juanes and Conover 1995); yet the possibility that juveniles also utilize coastal ocean habitats as nurseries remains largely uninvestigated. While estuaries have been traditionally regarded as vital nursery habitats for juvenile marine fishes, due to their high productivity levels (average annual primary productivity in Chesapeake Bay = 408 g C $m^{-2}yr^{-1}$, Harding et al. 2002), adequate forage base, and structure affording predator refugia; shallow coastal ocean habitats of the Middle Atlantic Bight are also highly productive (360 g C $m^{-2}yr^{-1}$, Sherman et al. 1984) and likely possess an abundant forage base (e.g., *Anchoa* sp.), and could support nursery functions. Juvenile bluefish may utilize ocean habitats as nurseries to a similar or greater extent than estuaries. If so, then recruitment success is influenced by factors influencing growth and survival in both oceanic and estuarine nurseries; therefore, it is necessary to gauge relative contributions to annual recruitment associated with either nursery.

The broad goal of this thesis was to evaluate if coastal ocean habitats function as important nurseries for young-of-the-year (YOY) bluefish. The focal study area was shallow, ocean habitats (just outside the surf zone to 18 m depth) along the coast of Maryland, where monthly trawl sampling was conducted in 2003 (May – October) and 2004 (July – November). A comparative estuarine nursery habitat was also selected for study: the Chesapeake Bay, where samples were obtained in 2003 and 2004 from seining in littoral habitats and trawling in channel regions. I employed otolith microstructure analysis to age juvenile bluefish (n = 450 across habitats) for purposes of estimating hatch dates and growth rates, and performed diet analyses for c. 900 juveniles. My overall objective was to investigate and compare temporal recruitment patterns (hatch dates), growth rates, diet composition, and relative abundance (interannual, seasonal) of YOY bluefish within and between oceanic and estuarine nursery habitats.

A chief hypothesis of my study was that summer-spawned bluefish primarily recruit to and utilize coastal ocean rather than estuarine nursery habitats. Seasonal "spring" and "summer" cohorts of YOY bluefish result from major spawning peaks during spring (March-May, peaking in April) in continental shelf waters of the South Atlantic Bight and summer (July) in shelf waters of the Mid-Atlantic Bight. Juveniles recruit to near-shore nursery habitats from offshore, oceanic production areas. Recruitment dynamics of juveniles has been well-studied in estuarine habitats, where the spring cohort has been shown (via direct ageing analyses) to dominate YOY abundance, with minimal and inconsistent contribution of the summer cohort (Nyman and Conover 1988; McBride et al. 1993; McBride et al. 1995). Because reported larval densities are much higher for the summer cohort (Collins and Stender 1987; Smith et al. 1994), and these larvae are produced more proximate to near-shore nursery habitats (Smith et al. 1994) during relatively warm summer months (enabling rapid growth); the lack of strong recruitment of this cohort to estuaries is unexpected. Kendall and Walford (1979) and Able and Fahay (1998) proposed that summer-spawned bluefish may primarily recruit to coastal ocean habitats. Here, I used otolith-based ages to assign cohort membership to collected YOY bluefish, and compared relative cohort contributions within and between Maryland coastal waters and Chesapeake Bay (Chapter 1).

Growth rates are often used as a surrogate of nursery habitat value (Sogard 1992). In Chapter 1, I estimated cohort-specific growth rates of YOY bluefish to evaluate the following hypotheses: 1. Growth rates are higher for juvenile bluefish in Maryland coastal waters than those inhabiting Chesapeake Bay, and 2. The summer cohort exhibits higher growth rates than the spring cohort in ocean habitats. Variation in cohort growth rates has important implications for year class success. Previous research has concluded that primarily spring-spawned juveniles successfully recruit to the adult population, based on back-calculated sizes at age 1 (Chiarella and Conover 1990; Conover et al. 2003).

However, these studies assumed constant growth rates between cohorts, with the corollary that the spring cohort would be twice as large v. the summer cohort at the end of the summer growing season. The authors suggested that the lack of summer cohort contribution to the adult stock was higher due to overwintering mortality of that cohort in comparison to the spring cohort. It is possible though that growth rates vary between cohorts within and among nursery habitats; perhaps summer-spawned bluefish exhibit rapid growth in coastal ocean habitats and attain relatively large sizes by fall. I explore this possibility by estimating cohort growth rates and examining cohort-specific size distributions in coastal ocean habitats throughout the summer growing season and during early fall.

A principal criterion of nursery habitats that are "optimal" or "essential" to production of juvenile fishes is the adequacy of the available forage base, with respect to both abundance and size. Of particular importance in sustaining juvenile bluefish is the availability and encounter with piscine prey, because juvenile bluefish are capable of nearly complete piscivory upon recruitment to nursery habitats (Marks and Conover 1993). Further, growth rates of juvenile bluefish have been shown to be higher on a fish v. invertebrate diet (Juanes and Conover 1994a); therefore, habitats with abundant and diverse fish prey would be expected to afford higher growth and survival of juveniles, which may ultimately translate into recruitment success.

In Chapter 2, I evaluated interannual, seasonal, cohort, and spatial (depth) patterns of diet composition of juvenile bluefish within and between Maryland coastal waters and Chesapeake Bay. Interannual and seasonal availability (abundance) trends of principal prey were examined. Of particular interest were the relative abundance levels of bay anchovy in coastal ocean environments. Bay anchovy may represent a potentially important component of piscivorous food webs in coastal habitats as well as estuaries, but abundance levels and size distributions during summer in ocean habitats are largely unknown. I hypothesized that relative abundance of bay anchovy was equivalent or higher in coastal ocean v. estuarine environments. I also explored size selectivity and predator-prey size relationships of bluefish and bay anchovy prey in coastal ocean habitats.

# CHAPTER 1

## RECRUITMENT DYNAMICS AND GROWTH OF JUVENILE BLUEFISH IN MARYLAND COASTAL WATERS AND CHESAPEAKE BAY

Abstract: Juvenile bluefish are considered to be estuarine dependent, but may recruit to and utilize coastal ocean environments as nurseries, in addition to estuaries. This study investigated cohort recruitment dynamics and growth rates of young-of-the-year bluefish in Maryland's shallow ocean habitats (2003 – 2004), and contrasted oceanic recruitment and growth patterns with those in a major estuarine system, Chesapeake Bay. Hatch dates and growth rates were estimated from ages obtained by otolith microstructure analysis. Hatch dates generally peaked in spring (April-May) and summer (July) across systems and years. However, specific recruitment patterns differed between years in the coastal ocean, where hatch dates were strongly bimodal (with a June gap) in 2003, but semi-continuous in 2004, when distinct "spring" and "summer cohorts" were less evident. The presence of June recruits and semi-continuous hatch dates in 2004 suggests that bluefish spawning may not be strictly pulsed. Both spring and summer cohorts were prevalent in coastal ocean habitats, yet immigration/emigration estimates suggested habitat use of the spring cohort was transient. In Chesapeake Bay, the spring cohort dominated and the summer cohort was rare. Growth rates of juvenile bluefish were equivalent or higher in ocean v. estuarine habitats. Within ocean habitats, growth rates were especially high for the summer cohort, ranging from 2.0 to 2.4 mm $d^{-1}$. My results suggest that coastal ocean environments may provide superior nursery habitats for summer-spawned bluefish than estuaries.

## Introduction

Shallow oceanic waters can function as important nursery habitats for many juvenile marine fishes that are often assumed to exclusively rely on estuaries during early life. Many coastal-spawning fish species of recreational and commercial importance along the eastern seaboard of the United States (e.g., bluefish; Atlantic menhaden, *Brevoortia tyrannus*; black sea bass, *Centropristis striata*) are considered to be "estuarine dependent" (McHugh 1967) or obligate estuarine users (Ray 1997). This classification is typically based on the occurrence of juveniles in estuaries (Able 2005; Able and Fahay 1998; Ray 2005) and supported by the dogma of estuaries as vital nursery habitats. However, the possibility that juveniles also recruit to and utilize coastal ocean environments as nurseries remains largely uninvestigated. Able (2005) states: "We often lack the comparative data on habitat use by fishes in the coastal ocean v. the estuary to make judgments about estuarine dependency".

The overall "value" of a particular nursery habitat is intangible and difficult to measure (Wilson et al. 2005), yet the theoretical foundation of relative value of nursery habitats is simple: namely, that habitats of higher value contribute disproportionately more individuals or biomass to the adult population (Beck et al. 2001; Kraus and Secor 2005). Separate metrics such as occurrence, density, growth, and mortality are often used an as index of juvenile production (nursery value) and compared between putative nursery habitats to evaluate their relative value (Able 1999). While these surrogates (especially growth rate) have often been compared between microhabitats (e.g. seagrass beds, oyster reefs, and macroalgae subtrates) within and among estuaries (Sogard 1992; Gibson 1994; Phelan et al. 2000; Ross 2003), only a few studies (Lenanton 1982; Able et al. 1995; Able et al. 2003) have considered the role of macro-scale coastal ocean habitats as potentially important nurseries. If juvenile fishes of some species utilize coastal ocean habitats as nurseries in addition to estuaries (i.e., they are facultative rather than obligate estuarine users), then it is important to evaluate the relative contribution of annual recruitments associated with either nursery.

Bluefish, *Pomatomus saltatrix*, is a migratory, continental-shelf species exhibiting a worldwide temperate and subtropical distribution (Juanes et al. 1996), with the exception of the East Pacific (Briggs 1960). The range of the Western Atlantic bluefish population is from southern Florida to Nova Scotia (Robins et al. 1986). Young-of-the-year (YOY) bluefish were considered to rely exclusively on estuaries as nursery habitats (McHugh 1967; Powles 1981; Friedland et al. 1988; Juanes et al. 1994; Juanes and Conover 1995; Munch 1997), however recent evidence suggests that juveniles may also utilize coastal ocean habitats as nurseries during the summer growing season. For example, Able et al. (2003) observed consistently high abundances in bottom trawl collections in inner continental shelf waters (5 – 27 m depth) off New Jersey during summer and early fall. Further, they noted that relative abundance in seine collections was one to two orders of magnitude higher in surf zone versus coastal lagoon environments. YOY bluefish have been documented in coastal ocean environments in Australia (Lenanton and Potter 1987) and South Africa (Smale 1984; Hutchings et al. 2002), and in surf zone habitats in Australia (Ayvazian and Hyndes 1995; Lenanton et al. 1996), South Africa (Clark et al. 1994), and Brazil (Barreiros et al. 2004).

Recreational and commercial fisheries exist for bluefish throughout its range (Juanes et al. 1996). This popular sport fish occurs along the entire Atlantic coast of the

United States, where it supports a major recreational fishery (Smith et al. 1994). A decline of recreational landings, spawning stock biomass, and fishery independent recruitment indices has occurred since the mid 1980s (Fig. 1.1) (ASMFC 2002). Accordingly, these indications of declining stock abundance have raised concern over the status of the stock and prompted a nine-year stock rebuilding plan (MAFMC 2005) and research addressing possible reasons for the decline. Priority research needs relevant to this study are investigating recruitment dynamics of juvenile bluefish (ASMFC 2002) and increased sampling of nearshore coastal zones (e.g. coastal ocean and surf zone habitats) to assess their relative value as nursery habitats (Fahay et al. 1999). Here, I examine recruitment patterns and growth rates of YOY bluefish in Maryland's coastal ocean environment, and compare oceanic recruitment dynamics and growth rates to those observed in a major estuarine system, Chesapeake Bay.

Bluefish eggs and larvae are produced at distances 100s of kilometers from near-shore nursery habitats, hence oceanographic processes play an important role in larval transport and delivery of juveniles to nurseries. Bluefish have a complex life cycle, and some debate exists over the specific spatiotemporal aspects of spawning activity and stock structure of the Western Atlantic population. Synoptic ichthyoplankton collections (MARPMAP surveys) indicate that spawning is protracted and advances northward in conjunction with the migration of adults from the South Atlantic Bight (SAB; shelf waters from Cape Canaveral to Cape Hatteras) in the spring (Collins and Stender 1987) to the Mid Atlantic Bight (MAB; shelf waters from Cape Hatteras to Cape Cod) in the summer (Smith et al. 1994). Spawning in the SAB occurs over the outer continental shelf from March to May and peaks in April, and also occurs at low-levels from September to

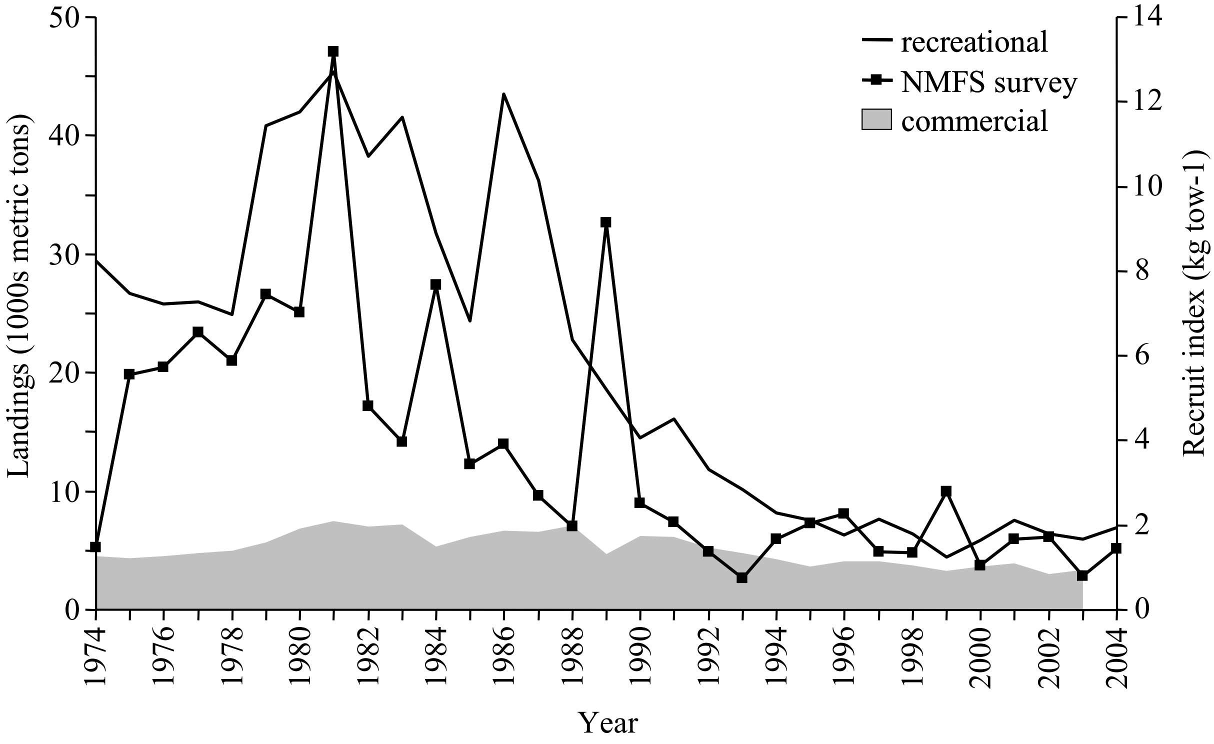


Figure 1.1. Time series of recreational and commercial landings of bluefish along the U.S. East Coast, and annual catch-per-unit-effort of bluefish (recruitment index) in the NMFS-NEFSC (National Marine Fisheries Service, Northeast Fisheries Science Center) fall bottom trawl survey, which occurs in shelf waters of the MAB during September-October. (data courtesy of NOAA: http://www.st.nmfs.gov/st1/recreational/queries and unpubl. data from ASMFC).

October coincident with the southern migration of the population during fall (Collins and Stender 1987). Spawning in the MAB occurs during late May through August and peaks in July (Smith et al. 1994; Norcross et al. 1974). This view of bluefish reproductive ecology suggests the presence of a single, migratory stock.

The alternative view of bluefish reproduction is that spawning is temporally discrete (Kendall and Walford 1979) with spawning episodes concentrated during April in the SAB and July in the MAB. Chiarella and Conover (1990) suggested the apparent paucity of bluefish spawning from mid-May to mid-June may result from a lack of spawning during the northward summer migration, which roughly coincides with this time period (Lund and Maltezos 1970). Meanwhile, Kendall and Walford (1979) proposed that temporally distinct spawning events were associated with two distinct bluefish stocks (sub-populations): one stock resident to the SAB that spawns during spring and fall and another stock, which spawns in the MAB during summer that undertakes seasonal inshore-offshore movements and overwinters in deeper shelf waters of the MAB (Lund and Maltezos 1970).

While some progeny from spring spawning in the SAB may recruit locally to estuaries of the SAB (Collins and Stender 1987; McBride et al. 1993), the majority are entrained in the Gulf-Stream current and advected northward to the MAB. Warm-core ring streamers are believed to be an important mechanism for transport of larvae from the Gulf Stream to the Slope Sea (the water mass between the continental shelf edge and the Gulf Stream) (Hare and Cowen 1996). Pelagic juveniles accumulate in the Slope Sea along the shelf-slope temperature front and begin their ingress across shelf waters when this thermal barrier dissipates in association with spring warming (Hare and Cowen

1996). Juveniles actively swim across the shelf to near-shore nursery grounds, and favorable (i.e., onshore) wind-driven surface flow also aids in cross-shelf transit (Munch 1997). Summer spawning in the MAB occurs in mid-shelf waters and shoreward (Smith et al. 1994), more proximate to shore versus spring spawning. Transport of summer-spawned larvae is influenced by longshore current in shelf waters, and juveniles actively swim to nursery grounds.

Recruitment of YOY to estuarine habitats along the US East coast has been well-studied (Nyman and Conover 1988; McBride and Conover 1991; McBride et al. 1993; Creaser and Perkins 1994; McBride et al. 1995). A consistent recruitment pattern has been observed whereby YOY arrive in two distinct pulses (June and August) of similar size fish with corresponding bimodal hatch dates (Nyman and Conover 1988; McBride and Conover 1991). The two modes observed in hatch date distributions ranged from March to mid-May with a peak in April and from mid-June to August with a peak in July; a gap was present during mid-May to mid-June. Two hypotheses have been put forth to explain this bimodal recruitment pattern: 1. Spawning occurs in two major episodes (spring in the SAB and summer in the MAB) and bimodal recruitment is simply a reflection of this temporally discrete spawning behavior (Nyman and Conover 1988; McBride and Conover 1991; Kendall and Walford 1979); 2. Spawning is protracted and the observed gap in hatch date distributions is a consequence of either low recruitment potential (due to unfavorable transport) of individuals produced in the southern MAB during mid-May to June (Hare and Cowen 1993) or else recruitment associated with this period occurs in regions where hatch dates have not been documented (e.g., Chesapeake Bay) (Smith et al. 1994).

Seasonal bluefish cohorts produced during the spring and summer are generally referred to as the "spring cohort" and "summer cohort." Higher abundance of the spring versus the summer cohort has been observed in estuarine habitats (Nyman and Conover 1988; McBride et al. 1993; McBride et al. 1995). Furthermore, studies focused on specific estuaries in New York and New Jersey (Nyman and Conover 1988; McBride and Conover 1991) have demonstrated that the spring cohort consistently recruits to estuaries and displays lower interannual variability in abundance than the summer cohort, which recruited to the same estuary in some but not all years.

Interestingly, Kendall and Walford (1979) proposed that most summer-spawned individuals remain in and utilize coastal ocean environments as nursery grounds rather than entering estuaries. High abundances of small juveniles (<100 mm) have been observed in shallow, oceanic waters off New Jersey during August and September; although these fish were not aged, they were presumed to represent the summer cohort (Able et al. 2003). Able et al. (2003) stated that: "Further examination, especially of the contribution of the summer-spawned cohort in ocean habitats, appears warranted."

Variation in cohort-specific growth rates of juvenile bluefish has important implications for year-class success. McBride and Conover (1991) observed that members of the spring cohort were two-fold larger in length than those of the summer cohort by the end of the first growing season (in estuaries), prior to the onset of the southerly fall migration to overwintering grounds (McBride and Conover 1991). Overwintering mortality can be size-selective (Sogard 1997) and migration costs would be expected to be disproportionately more taxing for smaller individuals. Hence, the smaller summer cohort might suffer higher mortality than the spring cohort during winter. The current recruitment index utilized for bluefish stock assessment is based on data from the National Marine Fisheries Service-Northeast Fisheries Science Center (NEFSC) fall bottom trawl survey, which is conducted in continental shelf waters of the MAB during mid-September through mid-October. Utilizing a length-based analysis of historical data from this survey, Conover et al. (2003) found that the summer cohort was more abundant than the spring cohort from 1992 to 2002, yet based on back-calculated lengths at age 1 (calculated from adult scale samples), the summer cohort appeared to contribute little to the adult stock. The authors suggested one possible reason for the lack of contribution from the summer cohort to the adult stock was higher overwintering mortality of the summer cohort relative to the spring cohort. Although cohort-specific growth rates and associated sizes attained at the end of the growing season have been well-studied in estuarine habitats (Nyman and Conover 1988; McBride and Conover 1991; McBride et al. 1993; Creaser and Perkins 1994; McBride et al. 1995), relatively few studies have evaluated cohort-specific growth (Takata 2004) and size structure (Able et al. 2003) in shallow, oceanic environments.

## *Objectives and Hypotheses*

My chief aim was to characterize cohort recruitment patterns and growth rates of YOY bluefish in a potentially important nursery habitat, the shallow coastal ocean < 20 m depth. Although the majority of data I collected in this study was obtained from sampling in Maryland's coastal ocean environment, I also examined samples and historical data from the Chesapeake Bay as a comparison nursery habitat. I employed otolith microstructure analysis to interpret daily ages of bluefish used to estimate hatch dates and growth rates. Specific objectives and associated hypotheses (bullets) were:

1. Determine temporal patterns of recruitment in Maryland coastal waters and Chesapeake Bay.

    - *Hypothesis 1.* Bimodal recruitment occurs in both oceanic and estuarine habitats.

2. Contrast the relative contribution of observed seasonal cohorts within and among coastal ocean and estuarine habitats.

    - *Hypothesis 2.* The summer cohort shows dominant representation in coastal ocean environments, whereas the spring cohort shows higher representation in estuarine habitats.

3. Evaluate system (i.e., coastal ocean v. estuary), cohort, and interannual differences in growth rates.

    - *Hypothesis 3.* The summer cohort exhibits higher growth rates than the spring cohort in both estuarine and coastal ocean habitats.
    - *Hypothesis 4.* Growth rates are higher for juvenile bluefish occurring in Maryland coastal waters than those inhabiting Chesapeake Bay.

## Materials and Methods

### Study Areas and Field Sampling

#### I. Coastal Ocean

The study area comprised shallow inner continental shelf waters (5 – 18 m) along Maryland’s coast. The total study area was approximately 150 km$^2$, encompassing waters immediately outside the surf zone to 6 – 7 km offshore (75$^o$ 10’15” – 74$^o$ 59’46”

W) and 22 km in an along-coast orientation south of the Ocean City Inlet and along the barrier island of Assateague ($38^o$ 18'37" – $38^o$ 08'13" N) (Fig. 1.2). This neritic zone exhibits low habitat complexity and a dynamic hydrological regime. The bottom type in this region is dominated by medium to fine grain sand (Wells 1994), and runnels and sand banks are common, especially in the southern portion of our sampling area (Conkwright and Gast 1995). Southern longshore currents are prevalent; wind and wind-driven waves typically approach this habitat from the southeast during summer (Hayes and Nairn 2004). Observed swell heights were generally less than 1 m. Water temperatures and salinity (averaged for the entire water column during sampling events) ranged 12.2 – 22.8 $^o$C and 25.1 – 32.0 during May – October 2003, respectively; 16.0 – 22.6 $^o$C and 29.6 – 31.4 during July – November 2004. Highest temperatures were observed in September 2003 and lowest temperatures in May 2003.

A gear change and minor modifications to my survey design were made between sampling years 2003 and 2004. The reason for this change was our research group's participation in NOAA's coast-wide, multi-investigator study on bluefish recruitment dynamics (BlueCoast). We switched gear types and modified our survey design in 2004 in accordance with the standard operating procedures agreed upon for the BlueCoast project: a large bottom trawl (Yankee survey trawl) and a depth-stratified survey design with two strata and equal allocation.

Based upon information that depth affected juvenile bluefish abundance in coastal regions (Takata 2004), I developed a depth-stratified simple random sampling survey design for both years of the study. The study area was delineated into three depth strata in 2003: shoal (5 – 9 m), intermediate (9.1 – 13.5 m) and deep (13.6 – 18 m); two strata

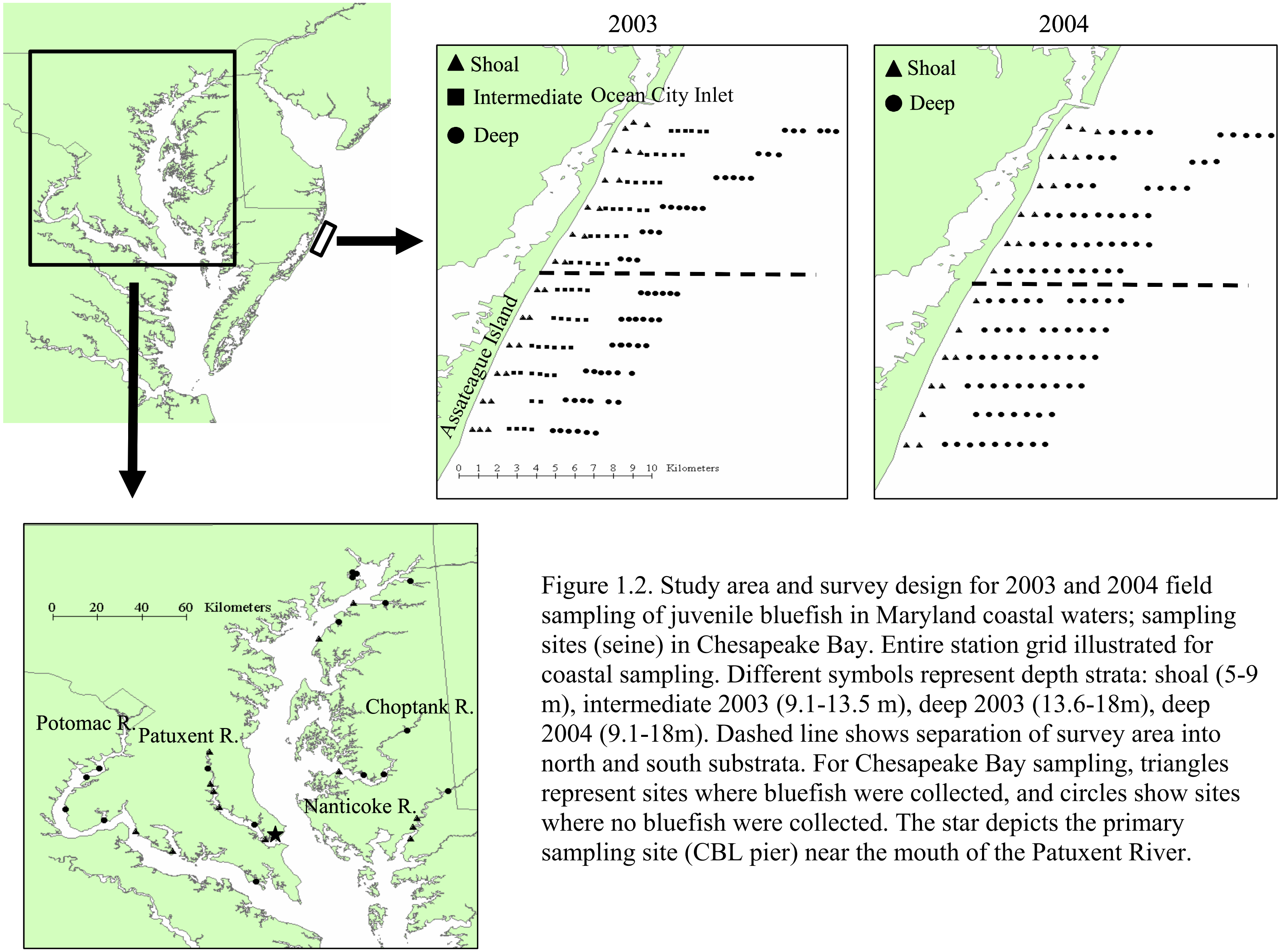


Figure 1.2. Study area and survey design for 2003 and 2004 field sampling of juvenile bluefish in Maryland coastal waters; sampling sites (seine) in Chesapeake Bay. Entire station grid illustrated for coastal sampling. Different symbols represent depth strata: shoal (5-9 m), intermediate 2003 (9.1-13.5 m), deep 2003 (13.6-18m), deep 2004 (9.1-18m). Dashed line shows separation of survey area into north and south substrata. For Chesapeake Bay sampling, triangles represent sites where bluefish were collected, and circles show sites where no bluefish were collected. The star depicts the primary sampling site (CBL pier) near the mouth of the Patuxent River.

in 2004: shoal (5 – 9 m) and deep (9.1 – 18 m). The intermediate and deep strata that I defined in 2003 were combined into one stratum (deep, 9.1 – 18m) in 2004 (Fig. 1.2). The dimensions of the narrow shoal stratum (~ 0.5 km wide and less than 1 km from shore) were the same each year. We attempted to sample the shallowest depths possible within this stratum contingent on sea state and vessel draft constraints. All potential stations (Fig. 1.2) in each stratum were plotted using CapN Voyager ©. The sampling unit was defined as an individual tow. To ensure independence of sampling units, adjacent stations were separated by at least 1 nautical mile along-coast; 300 m and 500 m in an east-west orientation for 2003 and 2004, respectively. The increased east-west separation in 2004 was due to the larger gear we employed that year.

The desired total sample size per cruise (2 vessel days) was 16 tows, and I used optimal allocation in 2003 and equal allocation in 2004 to assign sample sizes to each stratum. Takata (2004) provided bluefish catch data (years 2000 and 2001) from the same region that was used in the optimal allocation procedure, in which sample sizes were allocated according to the proportional sizes of strata variances (Thompson 2002):

$$n_h = \frac{nN_h\sigma_{yh}}{\sum_{h=1}^{L} N_h\sigma_{yh}} \qquad (1)$$

where $n_h$ is optimal number of stations in the sample from a particular stratum, n is the total sample size (16), $N_h$ is the number of potential stations in stratum h, and $\sigma_{yh}$ is the estimate (i.e., sample standard deviation) of stratum population standard deviation of bluefish catch-per-unit-effort. This allocation scheme resulted in allocation of five stations ($n_h$) in the shoal stratum, six in the intermediate depth stratum and five in the deepest stratum. An even number of sampled stations within each stratum was required because the study area was divided into north and south substrata (Fig. 1.2) for logistical reasons. Hence, four stations were allocated to the deep stratum and six stations each to the intermediate and shallow strata. In 2004, eight stations each (four per stratum for each cruise day) were allocated to shoal and deep strata. I used the random number generator in JMP © to select a random sample of stations within each stratum for each cruise from a universe of possible stations (Fig. 1.2).

We conducted seven monthly cruises in 2003 from late May through mid-October, using an 18 $m^2$ mouth-opening mid-water trawl with a 6 mm mesh cod end (Table 1.1). Sixteen stations were sampled during each two-day cruise, and additional tows were conducted in some months near the Ocean City Inlet to increase sample size. Each twenty minute tow sampled the entire water column by adjusting depth of deployment in 10 x 2 minute stepped intervals. We chartered the 42’ F/V *Leanna*, which deployed the net in most tows in a south-southwest direction; average tow speed was 2.5 knots.

In 2004, gear type and vessels were changed: large bottom trawls (Table 1.2) were deployed from the 55’ commercial dragger *Tony and Jan*. The majority of these tows were in a south-southwest direction with an average tow speed of 3.4 knots. Four monthly cruises were conducted from late July through early November (Table 1.1). Weather conditions postponed the date of our last cruise till early November, and the second day of this cruise was terminated early due to rough seas (~ 6 ft. swells). A commercial bottom trawl was used during the first two cruises and a Yankee survey trawl for the latter cruises. Gear characteristics were similar between trawls (Table 1.2). Nevertheless, mean opening height of the commercial trawl was significantly higher

Table 1.1. Sampling dates, gear type, and deployments in Maryland coastal waters. For 2004, number of tows of ten and twenty minute tow duration in each depth stratum reported; numbers in parentheses indicate the number of tows that were split to facilitate processing.

2003 – Mid-water trawl

| Cruise Date | Total No. Tows |
|---|---|
| May 28, 29 | 16 |
| June 24, 25 | 16 |
| July 8,9 | 16 |
| July 29, 30 | 16 |
| August 19, 20 | 18* |
| September 24, 25 | 18* |
| October 14 | 17* |

| 2004 – Otter trawl | | Shoal | | Deep | |
|---|---|---|---|---|---|
| Cruise Date | Total No. Tows | 10 min. | 20 min. | 10 min. | 20 min. |
| July 25, 27 | 16 | 7 | 1 | 7 | 1 |
| August 23, 24 | 12 | 2 | 4 | 3 | 3 |
| September 22, 23 | 16 | 4 | 4(2) | 4 | 4 |
| November 1, 4 | 10 | 1 | 5(2) | 0 | 4(1) |

* indicates extra tows were conducted at Ocean City Inlet to increase sample size (n = 2 in August and September, n = 1 in October)

Table 1.2. Gear specifications for the two different bottom trawls used during 2004 field sampling in Maryland coastal waters. Mean vertical spread (opening height) of each trawl was estimated from depth logger data (n = 11 tows for commercial trawl in August; n = 16 for Yankee survey trawl in September).

| | Trawl Type | |
|---|---|---|
| Specification | Commercial | Yankee |
| Headrope length | 87’ | 75.5’ |
| Footrope length | 103’ | 93.5’ |
| No. seams | 4 | 2 |
| Net material | Nylon | Polyethylene |
| Sweep | 2” rubber discs | 3’ rubber discs |
| Cod-end mesh size | 6.4 mm | 6.4 mm |
| Manufacturer | Trawl Works © | Gear Works © |
| Mean Opening Height | 3.4 m ± 0.51 SE | 2.6 m ± 0.44 SE |

(ANOVA, p = 0.0003) than that of the Yankee trawl (Table 1.2), likely resulting from its greater number of seams (Jeff Eutsler, personal communication). Our goal was to sample 16 stations per cruise and perform twenty minute tows, a sampling protocol similar to that used in 2003. However, we had very large catches during all cruises, requiring long processing times, which reduced the total number of stations that could be sampled in two days. For example, the average weight (± SE) per twenty minute tow in August was 564 ± 215.5 kg and 737 ± 201.4 kg in shoal and deep strata, respectively. Sciaenids (weakfish, *Cynoscion regalis*; Atlantic croaker, *Micropogonias undulatus*; spot, *Leostomus xanthurus*), butterfish *Peprilus triacanthus*, and anchovies (bay anchovy, *Anchoa mitchilli*; striped anchovy, *Anchoa hepsetus*) were common during all sampling months and comprised the bulk of large catches. We reduced the duration of some tows to ten minutes (July and August) to decrease the size of catches. Catches were generally lower in ten versus twenty minute tows; however, large catches were observed in some ten minute tows, especially in the deep stratum, apparently because of a patchy distribution of sciaenids. The total number of stations sampled and the number of ten and twenty minute tows conducted for each cruise were not consistent across cruises, yet they were similar in number between depth strata for a given cruise (Table 1.2). We conducted an equal number of ten and twenty minute tows in each stratum in September to systematically compare bluefish relative abundance (catch-per-tow) differences between tow durations.

A CTD (Conductivity-Temperature-Depth sensor) was cast prior to each tow in 2003 and 2004 to provide vertical profiles of water quality variables (temperature, salinity, dissolved oxygen), and a mini depth-logger (Vemco ®) was utilized to record and assess fishing performance of the trawl. All collected bluefish were enumerated and measured (total length, TL) to the nearest millimeter. We split the catches of some tows in 2004 to facilitate processing (Table 1.1), and either volumetrically estimated the number of bluefish collected in these tows (September cruise) or made direct counts of bluefish before splitting (November). We measured TL of the first 30 individuals for all other species (disk width for stingrays and skates) and either counted the remaining individuals or estimated the number caught by gravimetric subsampling. I preserved juvenile bluefish by placing them on dry ice. This "flash-freezing" method was used to minimize post-capture digestion (see Chapter 2) and ensure integrity of otoliths.

### *II. Chesapeake Bay*

Chesapeake Bay is the largest estuary in the United States and is a classified as a partially mixed, drowned river valley estuary. The Chesapeake Bay estuary exhibits greater habitat complexity (e.g. seagrass beds and oyster bars), shallower depths, and a much wider range of salinity and temperature in comparison to Maryland's coastal ocean habitats. About 50% of Chesapeake Bay is less than 6 m depth. Salinity ranges from < 0.5 at the head of the Bay to 32 at the mouth, and temperature usually peaks during late summer ($28 – 30^{o}$ C) and is lowest during winter ($1 – 4^{o}$ C) (Murdy et al. 1997). The Chesapeake Bay ecosystem includes a variety of habitats, from freshwater marshes to deep channels of the mainstem. Bluefish samples utilized for ageing in this study were collected in littoral zones (< 1.5 m depth) of sub-estuary tributaries (Patuxent, Potomac, Choptank, and Nanticoke Rivers) located in Maryland's portion of the Chesapeake Bay (Fig. 1.2).

All bluefish samples from Chesapeake Bay in 2003 were collected at the Chesapeake Biological Laboratory research pier (Fig. 1.2), whereas ancillary samples were obtained in 2004 from seining efforts by our group and Maryland DNR (Department of Natural Resources) (statewide survey). We conducted weekly seining with a 1.5 m x 30.5 m beach seine (with a bag) in 2003 (June 3 – October 8) and 2004 (May 13 – October 15). Temperatures during sampling periods ranged 17.5 – 29.5 $^{o}$C in 2003 and 20 – 28 $^{o}$C in 2004; salinity ranged 7.9 – 11.8 in 2003 and 5.6 – 12.2 in 2004. Three seine hauls were conducted on a single day each week on either side of the pier (one hour before low tide). In 2004, additional samples were obtained from June through August at sites upriver of the CBL pier in the Patuxent River (Fig. 1.2). Maryland DNR conducts monthly seine surveys (July – Sept) at sites throughout the Potomac, Patuxent, Choptank, and Nanticoke Rivers as well as the upper Chesapeake Bay (Fig. 1.2) (Maryland DNR, 2005). The gear used in this survey was a 30.5 m x 1.24 m bagless beach seine, and the deployment method was similar to that utilized by our group. Collected bluefish were enumerated, measured (TL, nearest mm) and frozen.

### *Subsampling for Ageing Analyses*

I subsampled preserved bluefish to provide representative subsets of juveniles to be directly aged via otolith microstructure analysis. Bluefish greater than 200 mm total length were not aged because the microstructure of otoliths from these larger fish was difficult to interpret, due to the presence of secondary growth centers and decreased contrast of peripheral increments (Takata 2004).

Subsampling protocols differed between years for bluefish collected in the coastal ocean. In 2003, I selected random samples of bluefish in proportion to their abundance in each length class (10 mm intervals). The subsampling unit (i.e., the pool of fish from which the random sample was drawn) for 2003 collections was all fish from a single station of a respective cruise. The overall sampling rate for 2003 was 56.2%: 122 of 217 juveniles less than 200 mm were directly aged. This high sampling rate was expected to yield a representative age composition of the juvenile “population” in our study area. Based on the high sampling rate, I assumed that a regression approach (predicting age from length) would be sufficiently representative of those individuals not directly aged.

We collected c. 3000 young-of-the-year bluefish during 2004 in Maryland coastal waters. A 50% sampling rate was not feasible for this number of fish; therefore, I constructed age-length keys (see Hatch Date Analysis) to characterize the population age composition. I used fixed-age subsampling for 2004 collections, whereby an equal number of specimens were randomly selected from each size class. Ketchen (1949) suggested that fixed-age subsampling was superior to random age subsampling (my method in 2003) for the development of age-length keys because individuals at the extremities of the size distributions are better represented in the subsample.

The 2004 subsampling unit was all juveniles collected from each stratum/substratum combination of respective cruises. Fish from the four different stations within each stratum/substratum combination (shoal/North, shoal/South, deep/North, deep/South) were given a unique pectoral fin clip scheme to maintain station identification. Subsequently, fish were measured and placed into 20 mm size bins, mixed, and a random sample was taken from each size bin. Four fish were subsampled for diet (Chapter 2), of which 2 were selected for otolith analysis. I repeated this procedure for all stratum-substratum combinations for each cruise to meet my laboratory analysis goals of 240 otoliths and 480 stomachs. If fish from a given size bin were lacking (i.e., < 4 fish) from a particular stratum-substratum combination, then the residual number of required fish of that size bin were selected from another substratum-stratum combination for that cruise. If no fish were present in a particular size bin for a given cruise then the number of samples selected from each size bin was scaled up so that the number of fish selected from each size bin was distributed as equally as possible across size bins to maintain the target sample size for the cruise (~64). This procedure resulted in 248 bluefish being selected for otolith analysis in 2004.

I aged all juvenile bluefish (n = 15) collected in Chesapeake Bay during 2003. Sixty-eight percent of juveniles (62 of 91) collected during 2004 in Chesapeake Bay were selected for ageing, including 30, 20, and 12 fish from CBL pier, Maryland DNR, and Patuxent River seine surveys, respectively. Samples selected from each survey contained fish of various sizes collected throughout the entire sampling period.

### *Otolith Microstructure Preparation and Interpretation*

Otolith preparation methods followed those presented by Secor et al. (1992). Sagittal otoliths were removed, cleaned in deionized water, and stored in plastic culture trays. Otoliths were air-dried for at least two days (typically > one week) and baked overnight in a drying oven (35 – 40$^{o}$ C) to remove all moisture prior to embedding. I embedded both left and right otoliths in Struer’s epoxy resin and sectioned otoliths in a transverse plane using a low-speed Isomet saw. I used thermoplastic glue to affix sections to petrographic slides. Sections were ground using wet/dry sandpaper of various grit sizes (400, 600, 800, and 1200). I ground sections until the primordium and its associated inner-most rings became evident, flipped the section after heating on a hotplate, then ground the section further to obtain a "paper-thin" section. The section was flipped again and polished on a felt, metallographic cloth covered with a slurry of 0.3 μm alumina oxide. This "triple-grinding-polishing" technique produced sections of increased increment contrast and clarity (Fig. 1.3) relative to sections that were only flipped once and ground/polished to the core.

I viewed sections under a compound microscope with both transmitted and polarized light, as the latter enhanced the contrast of peripheral increments. Increment counts were made at 200 – 600 X magnification, and immersion oil was used to increase increment clarity. Daily increment formation has been validated for juvenile bluefish (Nyman and Conover 1988). I conducted blind triplicate increment counts for each otolith, which were independent and non-successive. Estimated age was adjusted by subtracting one day from the mean of counts because the first increment forms at hatching (Hare and Cowen 1994). I employed the quality control criterion that all counts for a given otolith must fall within 10% of the mean (Nyman and Conover 1988; Takata 2004); if this condition was not met a fourth count was conducted and the outlier count discarded. If the fourth count did not result in an acceptable range of increment counts, the otolith was excluded from analyses (n = 2 for this study).

I conducted a between-reader ageing comparison to evaluate potential ageing bias. Reference otolith sections (n = 30) were provided by Takata (2004), whose preparation and interpretation methods were congruent with those employed in my study.

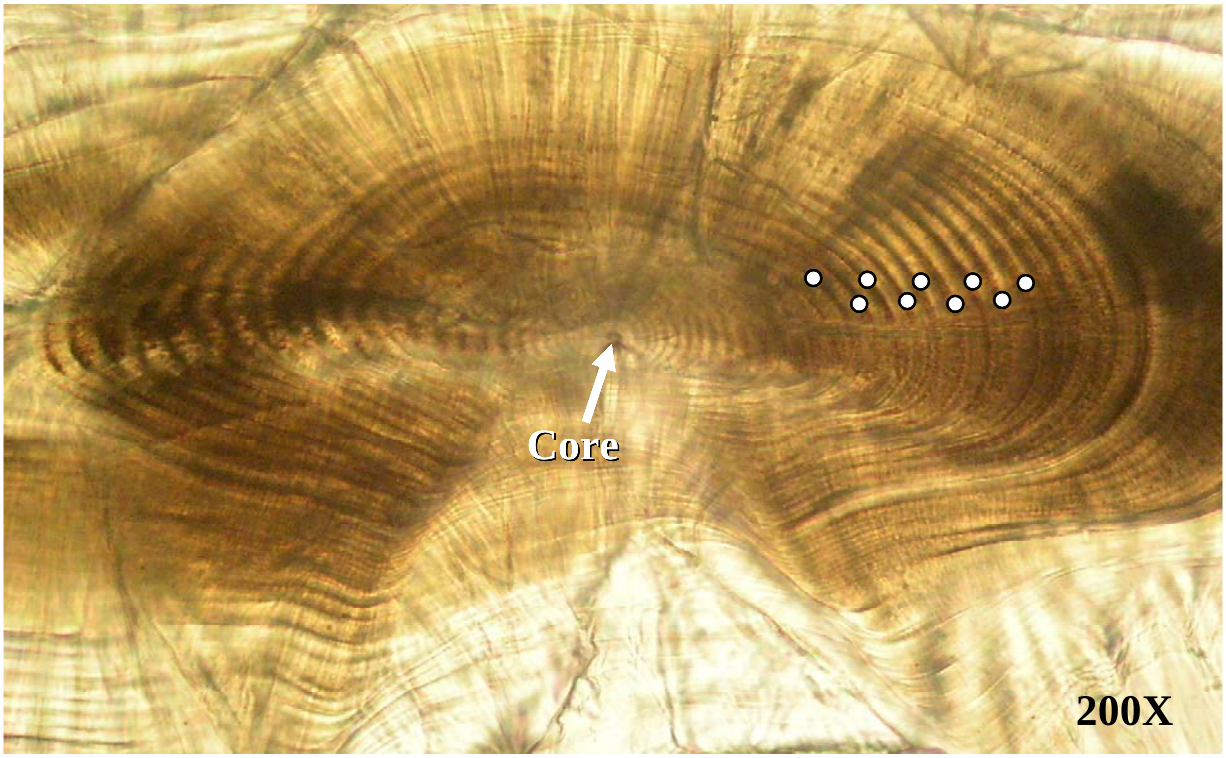


Figure 1.3. Thin section of sagittal otolith of juvenile bluefish at 200X magnification under transmitted light. Arrow indicates core; dots illustrate daily increments.

An age-bias plot (Campana et al. 1995) indicated no systematic ageing bias between readers (Fig. 1.4). The mean age difference between readers (0.02 days ± 0.61 SE) was not significantly different than zero (paired t-test, $p = 0.7$). The mean absolute difference, a measure of precision error, was 2.7 days ± 0.35 SE. Although consistently high between-reader agreement was observed and validates comparisons between results of this study and Takata (2004), between-reader agreement cannot be equated with ageing accuracy.

I assessed within-reader precision using the coefficient of variation (Campana et al. 1995):

$$CV_j = 100 \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j} \qquad (2)$$

where $X_{ij}$ is the $i^{th}$ age determination of the $j^{th}$ fish, $X_j$ is the mean age of the $j^{th}$ fish, and R is the number of times each fish is aged. The mean coefficient of variation of all aged individuals ($n = 447$) was 3.0%, and the range was 0 – 7.2%. The mean coefficient of variation was similar (ANOVA, $p = 0.6$) across age classes (45 – 70, 71 – 90, 91 – 110, 111 – 131 days), contrary to my expectation that the mean coefficient of variation would be higher (i.e., reduced precision) for older fish.

### *Hatch Date Analysis*

I examined hatch date distributions to identify seasonal bluefish cohorts recruiting to Maryland coastal waters and Chesapeake Bay across years. Hatch dates were calculated by subtracting mean daily age from date of capture. Due to the skewed nature of distributions, I calculated median hatch date values to determine peak hatch dates for

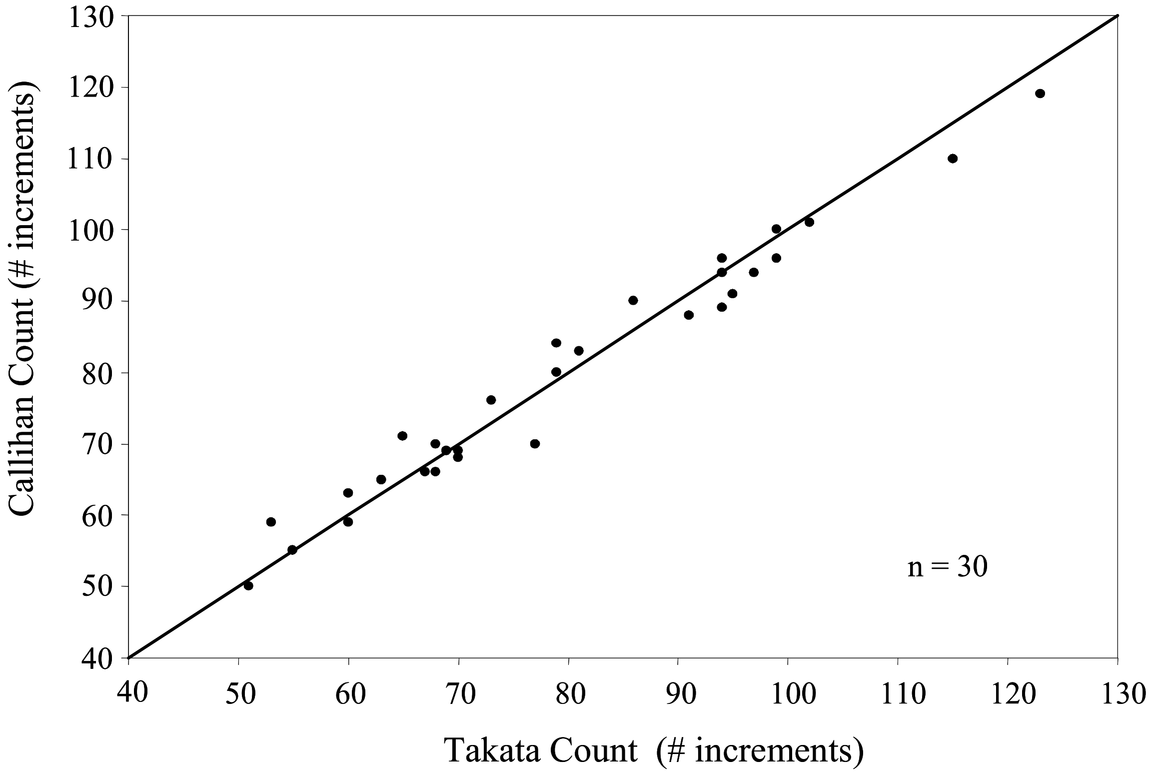


Figure 1.4. Age bias plot for between-reader ageing comparison of juvenile bluefish. Data points represent paired mean increment counts of readers for a given otolith. The solid 1:1 reference line indicates “perfect” agreement between readers.

respective cohorts. All system and year-specific hatch week distributions were non-normally distributed (chi-square tests of goodness of fit). Despite the lack of normality, there were clear gaps between at least two modal groupings (cohorts) for most distributions. Therefore, I used the NORMSEP procedure in FISAT II software to aid in cohort classification, although the assumption of normal component distributions (Abramson 1971) was not met. NORMSEP uses an iterative maximum likelihood technique to compute modal means and standard deviations. Modes must be separated by more than two standard deviations (the larger standard deviation of the two modes) to be considered distinct (Gulland and Rosenberg 1992). I then compared modal means of cohorts obtained through NORMSEP to calculated median values.

Composite hatch date distributions were obtained from summation of hatch dates of bluefish collected across cruises during a particular year. However, the number of tows differed between cruises (2003 and 2004), and in 2004, tow duration varied, and the number of ten and twenty minute tows were not evenly distributed within cruises across the field season (Table 1.1). Summation of hatch dates across unbalanced effort could yield biased hatch date distributions, skewed towards hatch dates of individuals collected in months with greater sampling effort. Hence, it was necessary to standardize monthly catches prior to application of age-length keys.

Individual lengths of bluefish were used to predict ages for those individuals not directly aged. Bluefish $\leq$ 200 mm that were directly aged are hereafter referred to as the "parental sample," while bluefish $\leq$200 mm whose ages were estimated are hereafter referred to as the "filial sample" (*sensu* Westrheim and Ricker 1978). Because parental samples were marked according to station, I accurately accounted for them (i.e., included them) in filial sample stations. Shrinkage effects were not estimated but were assumed to have the same relative effects across cohorts, size-classes, and age-classes. Some bluefish > 200 mm were classified as YOY (see below for further details), and ages of these larger YOY were estimated by cohort-specific age-at-length regressions.

In 2003, ages of filial samples, $\leq$200 mm, and YOY > 200 mm were estimated via cohort-specific least-squares linear regression derived from bluefish that were directly aged (n = 48 spring cohort, n = 74 summer cohort):

$$\text{Age} = 0.36*\text{TL} + 50.30,\ r^2 = 0.64 \quad \text{Spring Cohort 2003} \quad (3)$$

$$\text{Age} = 0.27*\text{TL} + 39.59,\ r^2 = 0.54 \quad \text{Summer Cohort 2003} \quad (4)$$

Decision of which age-length relationship (i.e., cohort) to apply was facilitated by analyzing monthly cohort lengths (see Results). In addition to the 16 standard tows in 2003, supplementary “inlet” tows were conducted (Table 1.1). For hypothesis testing, I excluded direct age estimates of bluefish collected from these tows. However, some (n=12) of these fish were directly aged, and their lengths and ages were included in the above regressions.

In 2004, monthly catches were standardized to the total number of YOY bluefish captured in 16 twenty minute tows (8 tows in each depth stratum, shoal and deep). Abundance multipliers for alternative tow durations (i.e., ten vs. twenty minutes) were based on systematic sampling in September, when an equal number of tows of ten and twenty minute duration (n = 4) were conducted within each depth stratum. Multipliers for YOY bluefish $\leq$200 mm were 1.99 and 1.73 in shoal and deep stratum, respectively;

and 1.60 for YOY of all sizes, irrespective of depth strata (Table 1.3). For those months with 16 tows, I used these multipliers directly to adjust catches in each 10 mm bin used in age-length keys. In August and November, fewer than 16 tows were performed; here, I adjusted the stratum-specific catch-per-unit-effort (CPUE) for bluefish $\leq 200$ mm to include deficit tows, using the mean stratum CPUE. As before, adjustments were made to account for 10 minute tows conducted during these months. Length frequency distributions were similar within stratum for a given cruise.

Abundances of YOY > 200 mm in 2004 were standardized using a similar procedure to that described above (adjusting for tow number and duration on each cruise). However, a 5 mm size interval for length bins was employed. Further, lengths were taken as the median of respective bins because ages of these larger YOY were estimated by regression rather than an age-length key, and the former requires an exact length.

Age-length keys were developed for each 2004 cruise (Tables 1.4 – 1.8) based on age-at-length data derived from directly aged fish $\leq 200$ mm (i.e., parental samples). Age-length keys for July and September incorporated age-at-length data pooled across depth strata because there was no significant difference in slopes of age-at-length between strata (ANCOVA, July: $p = 0.99$; September: $p = 0.97$). Separate age-length keys were constructed for August samples: one for the shoal stratum only (Table 1.5); another using data pooled across strata (Table 1.6), which was used to estimate ages of the filial sample from the deep stratum, because of low sample size and a non-significant linear regression of age on length for bluefish collected in the deep stratum ($p = 0.18$). The November age-length key was derived from age-at-length data from the shoal

Table 1.3. Comparison of YOY bluefish catches (mean CPUE) between ten and twenty minute tow durations of bottom trawl in Maryland coastal waters. Comparisons were made within two size classes of bluefish: juveniles ≤ 200 mm TL and YOY of all sizes (i.e., ≤ 300 mm TL). Four tows (Yankee trawl) performed for each stratum/tow duration combination. Stratum-specific tow multipliers for catches in 20:10 minute tow durations reported.

| | **Shoal** | | | **Deep** | | |
|---|---|---|---|---|---|---|
| | Mean CPUE ± SE | | | Mean CPUE ± SE | | |
| Size class | Ten | Twenty | Multiplier | Ten | Twenty | Multiplier |
| < 200 mm TL | 63 ± 26.1 | 126 ± 59.6 | 2.00X | 22 ± 5.0 | 34.2 ± 10.27 | 1.56X |
| All YOY | 98 ± 49.5 | 156 ± 68.7 | 1.59X | 27 ± 5 | 44 ± 11 | 1.63X |

Table 1.4. July 2004 age-length key. Upper limits of length intervals given. Parental number refers to the number of fish directly aged in each length class used to develop the age-length key. Proportions of bluefish (% of parental no.) reported for respective length classes. Filial number refers to the number of fish whose ages were estimated in respective length classes. Age refers to the mid-point of weekly age classes.

| | | | Age (days) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Total length (mm) | Parental no. | Filial no. | 53 | 60 | 67 | 74 | 81 | 88 | 95 | 102 | 109 |
| 80 | 2 | | 50.0 | 50.0 | | | | | | | |
| 90 | 2 | | | 50.0 | 50.0 | | | | | | |
| 100 | 2 | 1 | 50.0 | | 50.0 | | | | | | |
| 110 | 4 | 19 | | | | 75 | | 25 | | | |
| 120 | 18 | 11 | | | 16.7 | 22.2 | 44.4 | 11.1 | 5.6 | | |
| 130 | 5 | 13 | | | | 20.0 | 40.0 | 20.0 | 20.0 | | |
| 140 | 6 | 16 | | | | 16.7 | 33.3 | 50.0 | | | |
| 150 | 4 | 6 | | | | | 50.0 | 25.0 | 25.0 | | |
| 160 | 7 | 4 | | | | | 28.6 | 14.3 | 42.9 | 14.2 | |
| 170 | 3 | 2 | | | | | 33.3 | 33.3 | 33.3 | | |
| 180 | 4 | 2 | | | | | | 50.0 | 50.0 | | |
| 190 | 3 | 6 | | | | | | 33.3 | 33.3 | 33.3 | |
| 200 | 4 | 11 | | | | | | 50.0 | 25.0 | | 25.0 |

Table 1.5. August 2004, shoal stratum age-length key. Upper limits of length intervals given. Parental number refers to the number of fish directly aged in each length class used to develop the age-length key. Proportions of bluefish (% of parental no.) reported for respective length classes. Filial number refers to the number of fish whose ages were estimated in respective length classes. Age refers to the mid-point of weekly age classes.

| | | | Age (days) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Total length (mm) | Parental no. | Filial no. | 46 | 53 | 60 | 67 | 74 | 81 | 88 | 95 | 102 |
| 60 | 1 | 1 | 100.0 | | | | | | | | |
| 80 | 10 | 40 | 20.0 | 40.0 | 40.0 | | | | | | |
| 90 | 4 | 55 | | 75.0 | 25.0 | | | | | | |
| 100 | 7 | 21 | | 42.9 | 42.9 | 14.2 | | | | | |
| 110 | 2 | 18 | | 50.0 | 50.0 | | | | | | |
| 120 | 4 | 15 | | | 25.0 | 75.0 | | | | | |
| 130 | 4 | 27 | | | | 75.0 | 25.0 | | | | |
| 140 | 4 | 30 | | | 25.0 | 25.0 | 50.0 | | | | |
| 150 | 4 | 65 | | | | 25.0 | | 25.0 | | 25.0 | 25.0 |
| 160 | 1 | 116 | | | | | | | | 100.0 | |
| 170 | 4 | 127 | | | | | | 25.0 | 50.0 | | 25.0 |
| 180 | 2 | 64 | | | | | | | | 50.0 | 50.0 |
| 190 | 3 | 29 | | | | | | 33.3 | | 66.7 | |

Table 1.6. August 2004, pooled strata age-length key. Upper limits of length intervals given. Parental number refers to the number of fish directly aged in each length class used to develop the age-length key. Proportions of bluefish (% of parental no.) reported for respective length classes. Filial number refers to the number of fish whose ages were estimated in respective length classes. Age refers to the mid-point of weekly age classes.

| | | | Age (days) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total length (mm) | Parental no. | Filial no. | 46 | 53 | 60 | 67 | 74 | 81 | 88 | 95 | 102 | 109 |
| 60 | 1 | | 100.0 | | | | | | | | | |
| 80 | 10 | 1 | 20.0 | 40.0 | 40.0 | | | | | | | |
| 90 | 4 | 5 | | 75.0 | 25.0 | | | | | | | |
| 100 | 7 | | | 42.9 | 42.9 | 14.2 | | | | | | |
| 110 | 2 | 1 | | 50.0 | 50.0 | | | | | | | |
| 120 | 4 | | | | 25.0 | 75.0 | | | | | | |
| 130 | 4 | 1 | | | | 75.0 | 25.0 | | | | | |
| 140 | 4 | 3 | | | 25.0 | 25.0 | 50.0 | | | | | |
| 150 | 5 | 5 | | | | 20.0 | 20.0 | 20.0 | | 20.0 | 20.0 | |
| 160 | 4 | 3 | | | | | | | 50.0 | 50.0 | | |
| 170 | 8 | 8 | | | | | 12.5 | 25.0 | 37.5 | 12.5 | 12.5 | |
| 180 | 3 | 7 | | | | | | | | 33.3 | 33.3 | 33.3 |
| 190 | 8 | 5 | | | | | | 37.5 | 12.5 | 25.0 | 25.0 | |
| 200 | 1 | 2 | | | | | | | | | 100.0 | |

Table 1.7 September 2004 age-length key. Upper limits of length intervals given. Parental number refers to the number of fish directly aged in each length class used to develop the age-length key. Proportions of bluefish (% of parental no.) reported for respective length classes. Filial number refers to the number of fish whose ages were estimated in respective length classes. Age refers to the mid-point of weekly age classes.

| | | | Age (days) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Total length (mm) | Parental no. | Filial no. | 60 | 67 | 74 | 81 | 88 | 95 | 102 | 109 |
| 100 | 2 | 1 | 50.0 | 50.0 | | | | | | |
| 110 | 2 | 13 | 50.0 | 50.0 | | | | | | |
| 120 | 10 | 98 | 10.0 | 60.0 | 20.0 | 10.0 | | | | |
| 130 | 7 | 280 | | 42.8 | 28.6 | 28.6 | | | | |
| 140 | 7 | 208 | | 57.1 | 42.9 | | | | | |
| 150 | 6 | 93 | | 50.0 | 50.0 | | | | | |
| 160 | 5 | 44 | | 40.0 | 20.0 | 20.0 | 20.0 | | | |
| 170 | 3 | 45 | | | | 33.3 | 66.7 | | | |
| 180 | 8 | 34 | | | | 75.0 | 12.5 | 12.5 | | |
| 190 | 6 | 61 | | | | | | 83.3 | 16.7 | |
| 200 | 7 | 42 | | | | | 42.9 | | 42.9 | 14.2 |

Table 1.8. November 2004, shoal stratum age-length key. Upper limits of length intervals given. Parental number refers to the number of fish directly aged in each length class used to develop the age-length key. Proportions of bluefish (% of parental no.) reported for respective length classes. Filial number refers to the number of fish whose ages were estimated in respective length classes. Age refers to the mid-point of weekly age classes.

| | | | Age (days) | | | | | |
|---|---|---|---|---|---|---|---|---|
| Total length (mm) | Parental no. | Filial no. | 67 | 74 | 81 | 88 | 95 | 102 |
| 130 | 2 | | 50.0 | | 50.0 | | | |
| 140 | 2 | 2 | | 100.0 | | | | |
| 150 | 12 | 7 | 8.3 | 25.0 | 50.0 | 16.7 | | |
| 160 | 9 | 14 | | 44.4 | 33.3 | 22.3 | | |
| 170 | 7 | 15 | | 14.3 | 57.1 | 28.6 | | |
| 180 | 9 | 1 | 11.1 | 11.1 | 33.4 | 22.2 | 22.2 | |
| 190 | 5 | 3 | 20.0 | 20.0 | | 40.0 | | 20.0 |
| 200 | 5 | | | | 20.0 | 40.0 | 40.0 | |

stratum (n = 51) only, because all bluefish $\leq$ 200 mm collected in the deep stratum were directly aged (n = 5).

I used 10 mm size bins and weekly age bins for the construction of age-length keys. Age frequencies were calculated by multiplying the number of filial samples in a given length bin by the proportion of the total fish in each age class represented in the corresponding length bin of the parental age-length key. Age-length keys were applied separately to filial samples collected on different days of a respective cruise to facilitate accurate estimation of hatch dates. Daily ages were assigned as the mid-point of predicted weekly ages derived from age-length keys (e.g., if predicted ages = 64 – 70, then all bluefish would be assigned an age of 67 days). Finally, I used linear regression to predict the ages of some fish whose lengths were not represented in parental age-length keys (August: n = 8 from 65 to 70 mm, n = 54 from 190 to 200 mm; September: n = 2 at 74 mm):

$$\text{Age} = 0.41*\text{TL} + 20.4,\ r^2 = 0.83 \qquad \text{August, shoal stratum} \qquad (5)$$

$$\text{Age} = 0.35*\text{TL} + 27.85,\ r^2 = 0.69 \qquad \text{September, deep stratum} \qquad (6)$$

Estimated hatch dates obtained from the application of age-length keys (n = 3075) and regression (n = 64) were combined with hatch dates derived from direct ageing (n = 248) to generate aggregate hatch dates of individuals less than 200 mm that were used in hypothesis testing.

It is likely that some bluefish larger than 200 mm observed in collections (especially during late summer and fall) were young-of-the-year (YOY); however, these fish were not directly aged. Excluding YOY larger than 200 mm could potentially bias the interpretation of hatch date analyses, particularly the relative contribution and observed hatch peaks for the spring cohort. Few bluefish larger than 200 mm were collected in 2003 (n = 3 in September, n = 51 in October). Upon examination of their otoliths under a microscope, none exhibited an annulus. Further, I evaluated the otolith weight v. fish length relationship, under the assumption that yearling otolith weights would deviate (be heavier) from the overall relationship (Fig. 1.5). No such evidence occurred for 2003 juveniles. Hence, I classified all bluefish collected in 2003 as YOY. Age estimates for individuals larger than 200 mm were estimated from linear regression (equation 3).

Fish larger than 200 mm were common in 2004. I viewed whole otoliths of 29 fish, ranging 209 to 305 mm TL, collected during the later September cruise. A single individual larger than 300 mm displayed an annulus. The otolith weight:fish length value for this fish was clearly an outlier (Fig. 1.5) relative to the relationship for YOY fish. Hence, I classified all bluefish less than 300 mm TL collected in September and November cruises as YOY. For earlier July and August cruises, I used the estimated growth rate of the spring cohort in 2004 to estimate potential monthly maximum size criteria for YOY fish; this resulted in size cutoffs of 242 mm in August and 187 mm in July. Fish less than 200 mm collected during July did not posses an annulus; therefore, I classified fish $\leq$ 200 mm TL in July and $\leq$ 250 mm TL in August as YOY. Age estimates for individuals larger than 200 mm (August: n = 189, September: n = 381, November: n = 123) were estimated from linear regression of age at size for spring-spawned individuals that were directly aged (n = 93):

$$\text{Age} = 0.28*\text{TL} + 44.62,\ r^2 = 0.54 \qquad \text{Spring Cohort 2004} \quad (7)$$

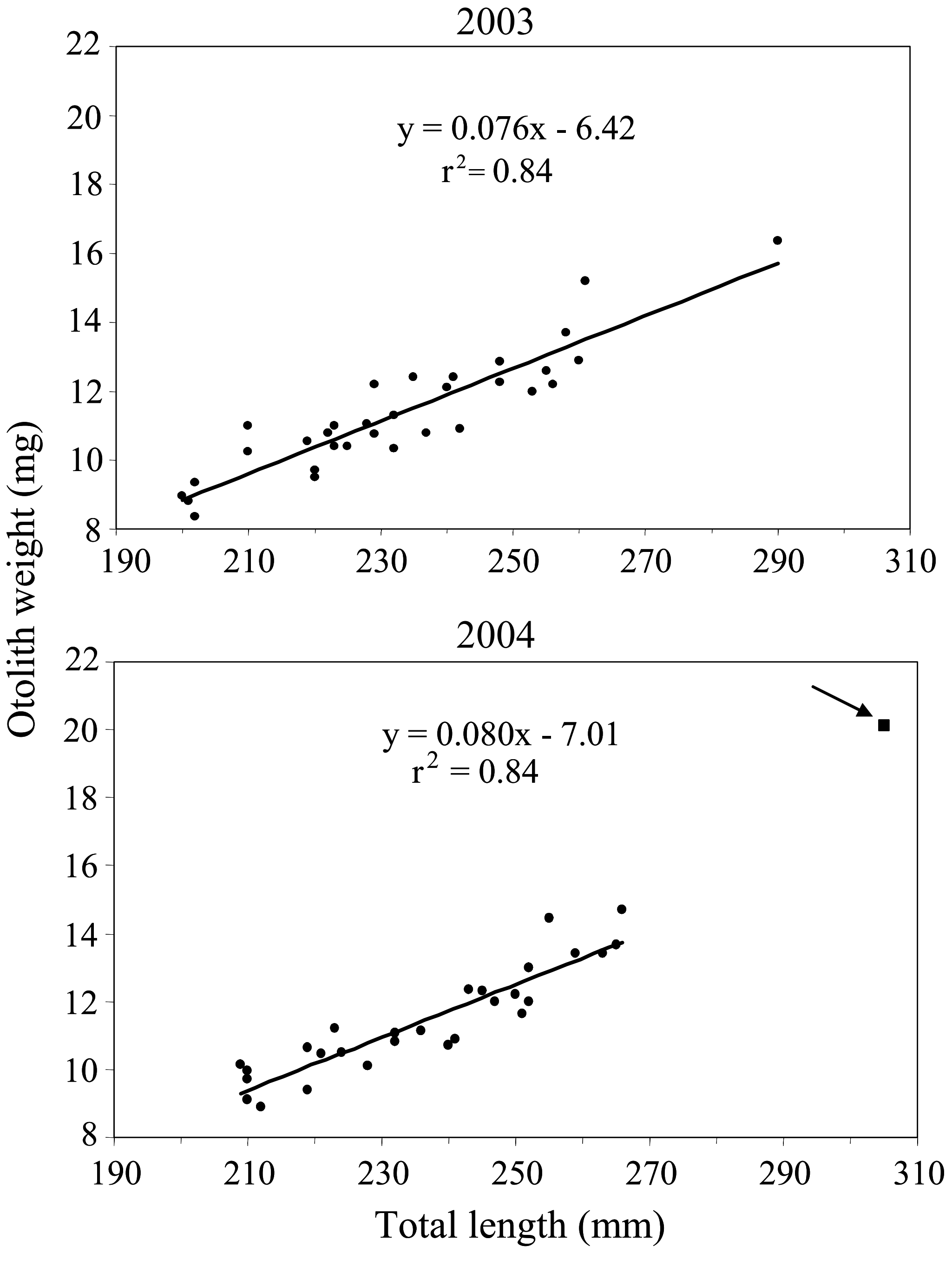


Figure 1.5. Otolith weight v. fish length relationships for YOY bluefish in 2003 and 2004. Arrow in 2004 plot indicates outlier which represents an age 1+ fish.

Other studies utilized similar size criteria to distinguish YOY and yearlings in fall sampling. Munch and Conover (2000) and Munch (1997) classified all fish less than 300 mm fork length (FL) collected during September and October as YOY.

Hatch date distributions were corrected for cumulative mortality bias. The premise for this correction is that older individuals collected on a particular sampling date will have experienced greater cumulative mortality than younger individuals. Therefore, unless cumulative mortality differences are considered, the frequency of older fish will be under-represented in hatch date distributions. Natural mortality rates of juvenile bluefish are unknown. The majority of reported natural mortality rates for the YOY juvenile stage of marine fishes range from 0.01 – 0.03 (Table 1.9). I used a conservative estimate of 0.01 for bluefish in my calculations because predation, the largest single cause of mortality during the juvenile stage (Houde 2002), is probably relatively low for bluefish. Additionally, I assumed that M was constant, although size- or age- specific M may be more realistic.

A standardized capture date is required to apply the cumulative mortality adjustment (Campana and Jones 1992). My goal was to correct for differential cumulative mortality experienced by all juvenile bluefish throughout the entire sampling period of a particular year. In this procedure, the final sampling date in respective systems and years was used as the standardized capture date (e.g., October 14 in the coastal ocean during 2003). Using the simple exponential decay model, I reduced the number of juveniles observed in each daily age bin on respective cruise dates by the number of days elapsed between collection and the standardized capture date. For example, those individuals collected on July 8 were exposed to 98 days of mortality

Table 1.9. Reported values of daily instantaneous mortality rates (M) during the juvenile period of marine fishes. Some studies estimated M in different years (indicated by multiple records for the same species and study).

| Species | M ($day^{-1}$) | Method | Study |
|---|---|---|---|
| American shad | 0.0027 | Lit. review | Bradford 1992 |
| Plaice | 0.003 | Lit. review | Bradford 1992 |
| Striped bass | 0.004 | Lit. review | Bradford 1992 |
| Greater amberjack | 0.0045 | Catch curve | Wells and Rooker 2004 |
| Striped bass | 0.005 | Lit. review | Houde 1987 |
| Winter flounder | 0.0058 | Lit. review | Bradford 1992 |
| Ayu | 0.0097 | Lit. review | Bradford 1992 |
| Atlantic cod | 0.01 | Lit. review | Houde 1987 |
| Bay anchovy | 0.01 | Lit. review | Houde 1987 |
| California halibut | 0.0124 | Catch curve | Kramer 1991 |
| Atlantic herring | 0.015 | Lit. review | Houde 1987 |
| French grunt | 0.015 | Lit. review | Houde 1987 |
| Striped bass | 0.016 | Mark-recapture | Dorazio 1991 |
| Winter flounder | 0.0161 | Length-based model | DeLong et al. 2001 |
| Northern anchovy | 0.018 | Lit. review | Bradford 1992 |
| American shad | 0.0185 | Lit. review | Bradford 1992 |
| Walleye pollock | 0.02 | Catch curve | Yoklavich and Bailey 1990 |
| Plaice | 0.0245 | Lit. review | Bradford 1992 |
| Striped bass | 0.031 | Mark-recapture | Dorazio 1991 |
| Atlantic cod | 0.0312 | Lit. review | Bradford 1992 |
| Plaice | 0.0336 | Lit. review | Bradford 1992 |
| Winter flounder | 0.0389 | Lit. review | Bradford 1992 |
| Red snapper | 0.045 | Catch curve | Rooker et al. 2004 |
| Striped bass | 0.053 | Lit. review | Bradford 1992 |
| American shad | 0.065 | Catch curve | Hoffman and Olney 2005 |
| American shad | 0.07 | Catch curve | Hoffman and Olney 2005 |
| Gulf menhaden | 0.0075 – 0.0209 | Catch curve | Deegan 1990 |

(number of days from July 8 → October 14); I also added 98 days to their observed ages (i.e., ages on July 8). I repeated this procedure for all cruise dates for a given year, which resulted in a composite age frequency on the standardized capture date, to which the following cumulative mortality function was applied (Brown and Bailey 1992):

$$N_{i,j} = \frac{N_i}{e^{-M(i-j)}} \qquad (8)$$

where $N_{i,j}$ is the abundance of cohort of daily age i corrected for mortality, $N_i$ is the abundance of daily cohort age i on the standardized capture date not corrected for mortality, M is the daily instantaneous natural mortality rate, and j is the youngest age represented in the sample (i.e., the youngest observed age on the standardized capture date: 60 days in 2003; 67 days in 2004). Larval-stage mortality rate was assumed to be constant for all individuals (Campana and Jones 1992). Also, because the youngest observed ages were well into the juvenile stage, the daily instantaneous mortality rate I assumed (0.01 $\text{day}^{-1}$) should be representative of mortality during the juvenile period, although there likely exists variability about this value (e.g., between cohorts within or among years). Finally, I summed adjusted daily cohort abundances by hatch week to generate hatch date distributions, corrected for cumulative mortality, that were used in hypothesis testing.

I used the chi-square test of independence to compare relative cohort abundances between the coastal ocean and Chesapeake Bay within a given year and between years within a given system. Fisher's Exact Test was utilized if cells of contingency tables had expected counts less than 5. I evaluated the effects of correcting for cumulative mortality and incorporating larger young-of-the-year (>200 mm) on the interpretation of cohort representation patterns by conducting chi-square tests for the following scenarios: 1. only fish $\leq$ 200 mm (directly aged) and not corrected for cumulative mortality (M); 2. only fish $\leq$ 200 mm and M corrected; 3. all estimated YOY and M uncorrected; and 4. all estimated YOY and M corrected.

I estimated hatch dates on a monthly basis to discern if recruitment of juveniles to coastal ocean habitats was pulsed or continuous. Monthly hatch date frequencies (all size YOY) were adjusted for cumulative mortality differences within each month. I used the chi-square test of independence to test if hatch date distributions differed between months. If the relative frequencies of hatch dates were similar within bi-weekly bins among cruises, then pulsed recruitment was assumed, else recruitment was considered to be continuous. Secondly, I examined possible immigration or emigration of bluefish from respective cohorts to and from our study area. Abundance (standardized to total number of YOY captured in 16 twenty minute tows each month) of a particular cohort in a given month (e.g., June) was reduced by natural mortality ($M = 0.01 \text{ day}^{-1}$) experienced between months to generate an expected abundance for the following month (e.g., July). Increases to adjusted abundance were assumed to be immigration; decreases were assumed to be emigration. I used chi-square goodness of fit tests to test if observed numbers were different from expected numbers across months for respective cohorts in a given year.

### *Growth Rate Estimation*

I estimated growth rates for each bluefish cohort (fish $\leq$ 200 mm that were directly aged) as the slope of linear regressions of total length (TL – 2 mm) on age. Two mm was subtracted from TL to account for the size of larvae at hatching (Deuel et al.

1966). Alternative growth models were examined (e.g., instantaneous growth in both length and weight; power and logistic functions); however simple linear regression exhibited the best-fit and facilitated comparisons of my cohort growth rate estimates with other studies. I used analysis of covariance to test for cohort, system, and year differences in growth rates. I used the criterion that > 75% of all observations must lie within the range of overlap in covariate (age) values among independent variables. Otherwise, I truncated the size at age data to common covariate values for the comparison. If slopes were not significantly different, covariate adjusted means (intercepts) were compared to test if one cohort was larger at a common age versus another. The growth rate for the summer cohort in Chesapeake Bay in 2003 was not estimated due to low sample size (n = 5).

I compared coastal water temperatures to differences in cohort-specific growth rates and the appearance of cohorts. Daily surface water temperatures records at NOAA Buoy #44009 (c. 15 nautical miles northeast of our coastal ocean sampling region) were used; these records were highly correlated with matched daily records from our cruises (r = 0.83).

Conversions from total length (TL) to fork length (FL), for comparisons of maximum cohort sizes during fall with other studies, were made by the regression:

$$TL = 0.88*FL + 3.44 \quad (r^2 = 0.99,\ n = 403) \qquad (9)$$

## Results

### *Temporal recruitment patterns*

### *I. Coastal Ocean*

Composite hatch date distributions of bluefish from the coastal ocean were bimodal in 2003 (Fig. 1.6). Hatch date distributions of bluefish less than 200 mm TL were similar, with a nadir in hatch dates during mid to late June, regardless of cumulative mortality adjustment (Fig. 1.7), although modes were more discrete in the unadjusted distribution (Fig. 1.6), with a temporal gap June 14-28. Accordingly, I defined spring and summer cohorts in 2003 as those fish with hatch dates ranging from April to mid-June and from late June to mid-August, respectively (Table 1.10). Peak hatch dates of the spring cohort ranged from mid-April to early May, and the summer cohort from mid- to late July. Incorporation of hatch date estimates of YOY bluefish larger than 200 mm did not change the range of cohort hatch dates or observed paucity of hatch dates from mid- to late June (Fig. 1.6), but instead shifted the median hatch date of the spring cohort from early May to late May (Table 1.10).

The composite hatch date distribution in 2004 (regardless of cumulative mortality adjustment) was bimodal, yet the distribution was semi-continuous (Fig. 1.7); there was no obvious June temporal gap in hatch dates as was observed in 2003. I used the anti-mode (week interval of June 7) of the 2004 distribution as the division between spring and summer cohorts. I classified spring and summer cohorts as bluefish whose hatch dates fell prior to, and on or after June 10, respectively (Table 1.10). Hatch dates of spring and summer cohorts peaked in mid-May and late June to early July, respectively (Fig 1.6). Incorporation of hatch date estimates of YOY bluefish larger than 200 mm did

Fig 1.6. Hatch week frequencies of juvenile bluefish collected in Maryland coastal waters during 2003 and 2004. Top panels represent hatch date distributions based exclusively on direct ageing via otolith analysis (i.e., raw age data and no application of age length key, etc.). Bottom panels represent composite hatch date distributions derived from age estimation (e.g., cohort specific age at length regressions) of all YOY bluefish.

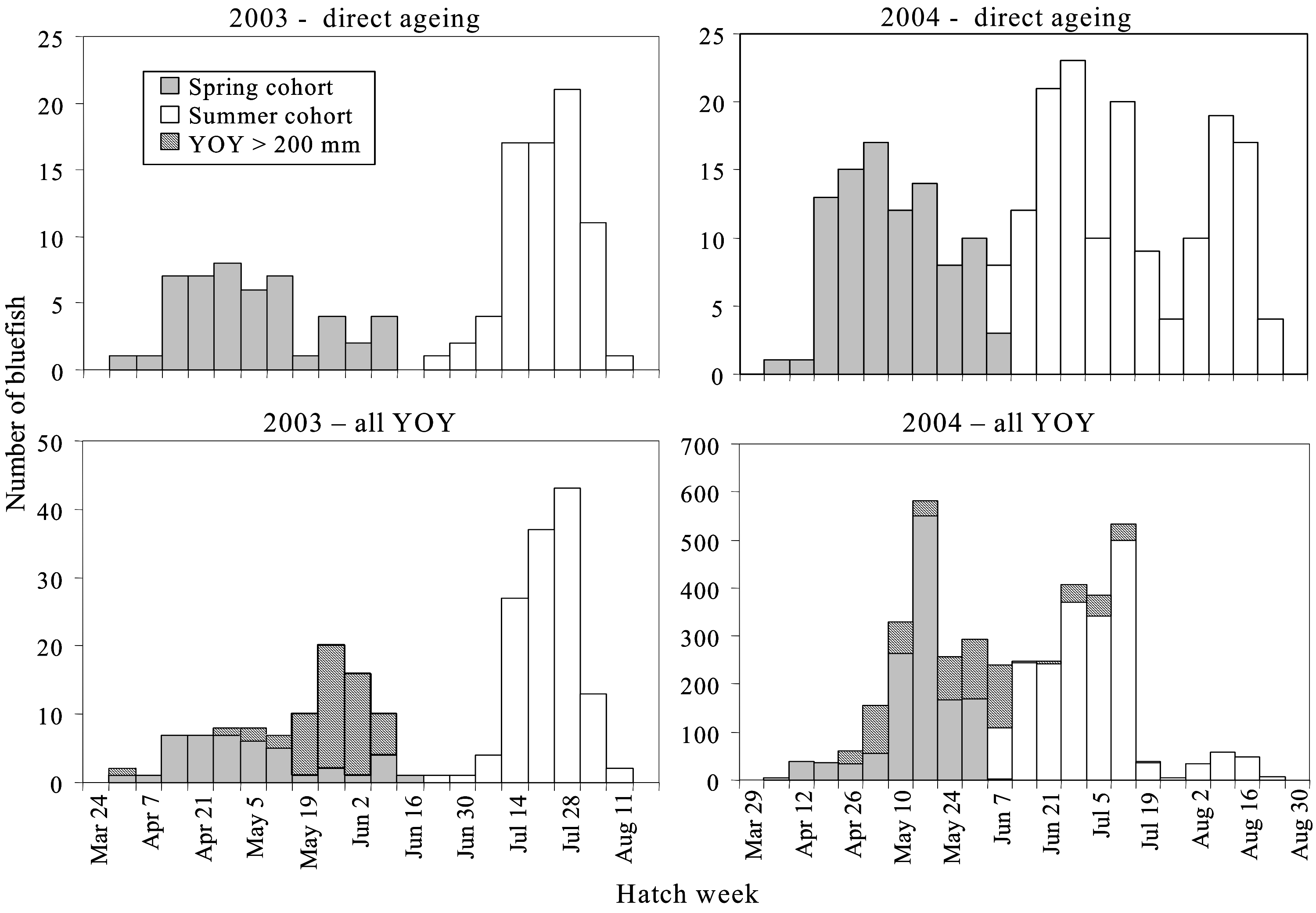


Figure 1.7. Hatch week frequencies of juvenile bluefish in Maryland coastal waters and Chesapeake Bay across years. Bars depict observed frequencies (no cumulative mortality correction), whereas solid lines represent frequencies corrected for cumulative mortality. Hatch date distributions of bluefish in the coastal ocean are shown separately for juveniles ≤ 200 mm and all YOY.

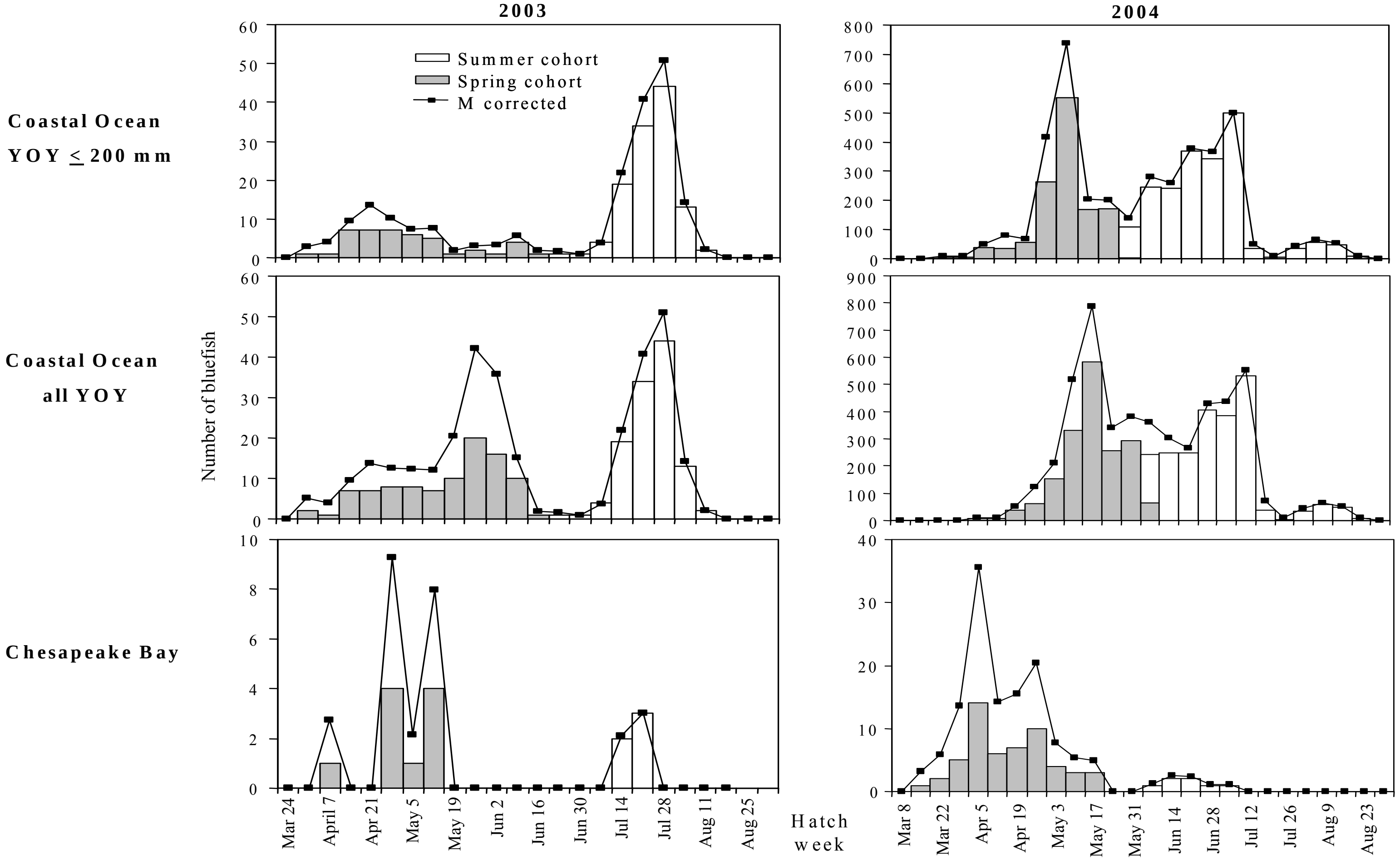


Table 1.10. Medians, means, and ranges of hatch dates of bluefish cohorts. Hatch date summary statistics reported for different inclusion scenarios (i.e., only bluefish ≤ 200 mm v. all sizes of YOY). For the subsampling column: direct age = only those individuals < 200 mm that were directly aged; ≤ 200 mm = directly aged individuals *and* those ≤ 200 mm TL whose ages were estimated via regression or an age-length key; all YOY = hatch dates estimates from larger YOY via regression (> 200 mm TL), integrated with data from the previous subsamples.

**Ocean 2003**

| Cohort | Subsample | Median | Mean | Range | n |
|---|---|---|---|---|---|
| Spring | direct age | May 5 | May 10 | April 6 – June 14 | 48 |
| Spring | ≤ 200 mm | May 4 | May 9 | April 6 – June 17 | 43 |
| Spring | all YOY | May 25 | May 22 | April 6 – June 17 | 97 |
| Summer | ≤ 200 mm | July 26 | July 25 | June 28 – August 15 | 128 |

**Ocean 2004**

| Cohort | | Median | Mean | Range | n |
|---|---|---|---|---|---|
| Spring | ≤ 200 mm | May 20 | May 18 | April 5 – June 7 | 1382 |
| Spring | all YOY | May 20 | May 20 | April 5 – June 9 | 1823 |
| Summer | ≤ 200 mm | July 7 | July 5 | June 10 – August 29 | 2005 |
| Summer | all YOY | July 5 | July 4 | June 10 – August 29 | 2189 |

**Chesapeake Bay 2003**

| Cohort | | Median | Mean | Range | n |
|---|---|---|---|---|---|
| Spring | direct age | May 5 | May 5 | April 13 – May 16 | 10 |
| Summer | direct age | July 22 | July 21 | July 18 – 23 | 5 |

**Chesapeake Bay 2004**

| Cohort | | Median | Mean | Range | n |
|---|---|---|---|---|---|
| Spring | direct age | April 18 | April 19 | March 18 – May 22 | 55 |
| Summer | direct age | June 23 | June 23 | July 12 – July 5 | 7 |

not change the range or median of cohort hatch dates, but rather reinforced the continuous nature of the distributions from late May to late June (Fig 1.6). Median and mean hatch dates of respective cohorts in a given year were similar and fell within the same week interval (Table 1.10). In both years, hatch date frequencies of the summer cohort declined precipitously after observed peaks, especially in 2004 (Fig. 1.6).

In 2003, juvenile bluefish were absent from May and June collections and the spring cohort was first observed during early July at sizes of 95 – 125 mm (Fig. 1.8) and ages of 72 – 91 days, with corresponding April hatch dates (Fig 1.6). The spring cohort was present at low-level abundances (CPUE < 1 $tow^{-1}$) from early July through September. The summer cohort was first observed in September at sizes of 70 – 150 mm and ages of 54 – 85 days (Fig. 1.8). The relative abundance of the summer cohort was at least two-fold higher than that of the spring cohort in September and October (Table 1.11). September and October length frequency distributions were bimodal, representing spring and summer cohorts in each month (Fig. 1.8). The mean size of the spring cohort (240 mm) was 100 mm larger than that of the summer cohort (140 mm) in October.

In 2004, the spring cohort was present during the first sampling cruise in late July. Sizes and ages of the spring cohort ranged from 71 – 200 mm (Fig. 1.8) and 54 – 111 days, respectively. High abundances of juvenile bluefish (> 100 $tow^{-1}$) were observed in August and September. Both spring and summer cohorts were present in late August, although the relative abundance of the spring cohort was c. 3-fold higher than the summer cohort (Table 1.11). Sizes and ages of the summer cohort in August ranged from 55 – 142 mm and 46 – 74 days, respectively. The summer cohort predominated in September and November (Fig. 1.8; Table 1.11). Length frequency distributions in 2004

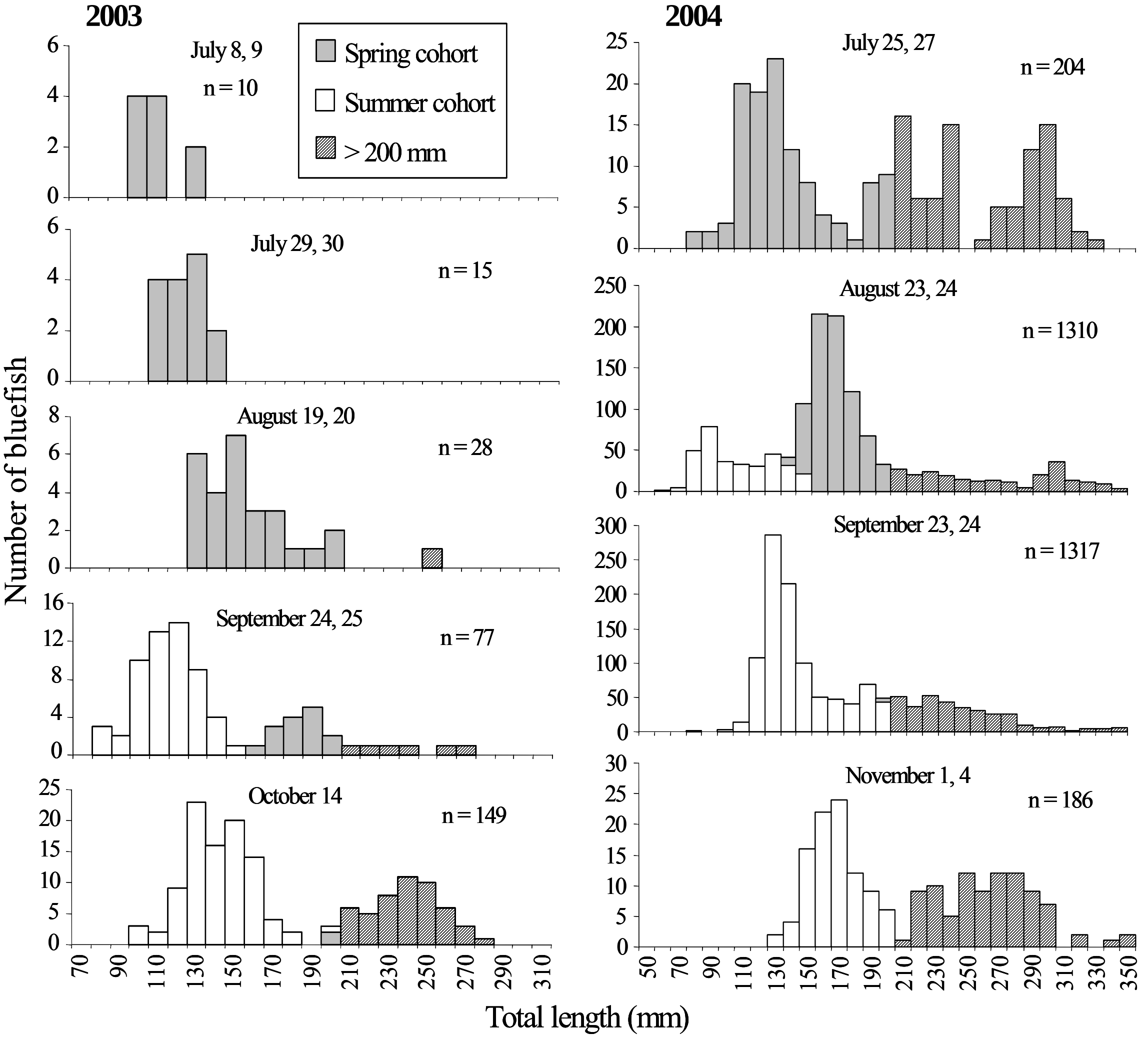


Figure 1.8. Cohort-specific (≤ 200 mm) length frequency distributions in the coastal ocean during 2003 and 2004. All bluefish ≤ 200 mm within a given length bin were assigned to a cohort based on direct age estimates of the subset of fish from the corresponding length bin that were directly age. Where both cohorts were present in a length bin, proportions of each in the age sample were used to estimate the numbers of each cohort. Note that cohort designations are not given for individuals larger than 200 mm (hatched bars) because these individuals were not directly aged. However, hatch dates estimated via regression indicated that all YOY > 200 mm in 2003 were spring-spawned bluefish; but in September 2004 represented both spring and summer cohorts and in November 2004, all YOY > 200 mm were summer-spawned bluefish (see Fig. 1.9). Maximum size of YOY bluefish assumed to be 300 mm TL each year.

Table 1.11. Relative abundance (mean catch-per-unit-effort ± SE) of spring and summer cohorts of YOY bluefish by cruise in Maryland coastal waters during 2003 and 2004. Catches in 2004 were standardized to number per twenty minute tow; monthly maximum size criteria of YOY were employed (see Methods).

| **2003** | | | **2004** | | |
|---|---|---|---|---|---|
| Cruise Date | Spring | Summer | Cruise Date | Spring | Summer |
| July 8,9 | 0.6 ± 0.34 | absent | July 25, 27 | 17 ± 4.5 | absent |
| July 29, 30 | 0.9 ± 0.44 | absent | August 23,24 | 72 ± 24.4 | 28 ±12.1 |
| August 19, 20 | 0.9 ± 0.81 | absent | September 23,24 | 31 ± 14.0 | 87 ± 21.0 |
| September 24,25 | 0.4 ± 0.16 | 1.9 ± 0.46 | November 1,4 | absent | 19 ± 6.0 |
| October 14 | 3.3 ± 1.71 | 5.8 ± 2.6 | | | |

did not closely track cohorts as did length modes in 2003. For instance, during August, minimal size overlap existed between spring and summer cohorts at lengths of 130 -145 mm (Fig. 1.8). Moreover, length distributions in November were bimodal (Fig. 1.8); however, all young-of-the-year had hatch dates corresponding to the summer cohort (Fig. 1.9), as no spring-spawned individuals were observed in November.

Hatch week distributions were significantly different among months for both spring and summer cohorts, regardless of year (Fig. 1.9) (2003 spring: $p < 0.0001$ Fisher's Exact Test; 2003 summer: $p < 0.0001$ Fisher's Exact Test; 2004 spring: $p < 0.0001$; 2004 summer: $p < 0.001$). Considerable overlap in hatch date ranges of cohorts between months was present. Nevertheless, mean hatch dates appeared to progress forward (generally one to two weeks later) from one month to the next, and ranges of cohort hatch dates did not strictly overlap between months (Fig. 1.9). For example, mean hatch dates of the spring cohort shifted two weeks forward from July to August in 2004. Additionally, bluefish with April hatch dates were common in July, but absent in August (Fig. 1.9).

Estimates of immigration/emigration were significant for the spring cohort in both years (2003: $p = 0.04$ across July to September; $p < 0.0001$ across all months; 2004: $p < 0.0001$ across all months) and the summer cohort in 2004 ($p < 0.0001$ across all months). The summer cohort in 2003 was not tested because this cohort was only present during one time period (September to October). In 2003, immigration of both cohorts was observed, irrespective of specific time periods (Table 1.12). For each cohort, the largest changes in abundance occurred from September to October (Table 1.12). Immigration of the spring cohort from late July to August and from August to September was minimal

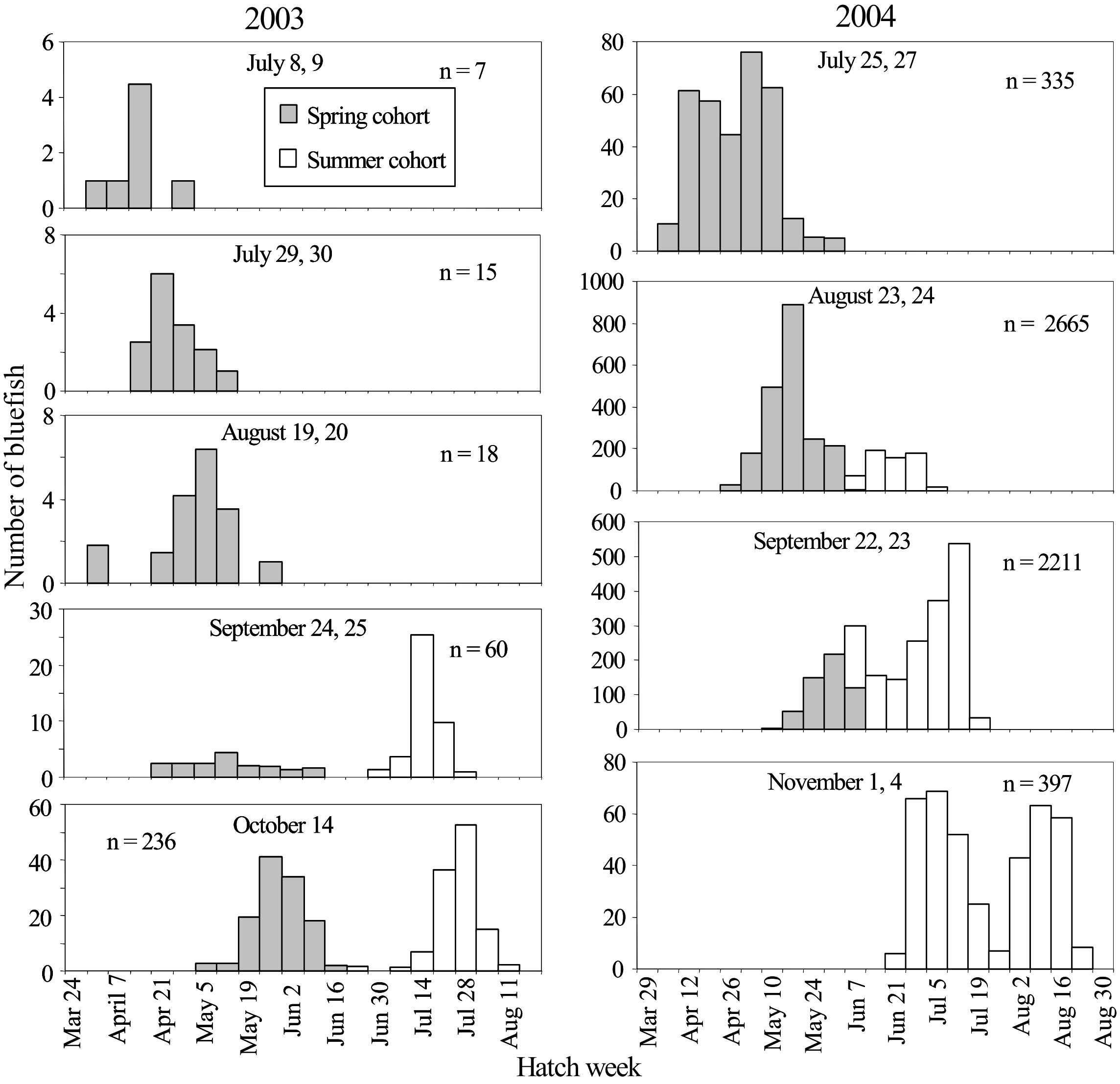


Fig 1.9. Hatch week frequencies of juvenile bluefish by month (cruise date) in Maryland coastal waters during 2003 and 2004. Hatch date estimates of all YOY bluefish included; hatch dates corrected for cumulative mortality differences within each month. n refers to the standardized total number of YOY bluefish observed each month, irrespective of cohort.

Table 1.12. Monthly immigration/emigration (I/E) estimates of bluefish cohorts in Maryland coastal waters during 2003 and 2004. Abundances (standardized to total number captured in 16 twenty-minute tows for 2004 data) of each cohort observed during a given cruise (O1 below, e.g., = 15 spring cohort bluefish on the July 29) were reduced by natural mortality experienced between months (M below = # deaths over this period assuming a daily instantaneous natural mortality rate of 0.01 $day^{-1}$) to generate an expected abundance (E below) for the following month (e.g., August 19). For I/E#: Immigration (positive) or emigration (negative) refer to the residual number of fish observed (where O2 = number actually observed the following month, I/E = O2-E) relative to the expected value. I/E% expresses the percentage of the number of individuals that immigrated or emigrated from one month to the next, respectively. These values (I/E%) were scaled such that +100% and -100% equate to complete immigration and emigration from one month to the next, respectively.

| **2003** | Spring Cohort | | | | | | Summer cohort | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Time period | O1 | M | E | O2 | I/E# | **I/E%** | O1 | M | E | O2 | I/E# | **I/E%** |
| Jul8 → Jul29 | 10 | 2 | 8 | 15 | 7 | **46.0** | N/A | | | | | |
| Jul29 → Aug 19 | 15 | 3 | 12 | 14 | 2 | **13.2** | N/A | | | | | |
| Aug 19 → Sep 24 | 14 | 4 | 10 | 11 | 1 | **11.2** | N/A | | | | | |
| Sep 24 → Oct 14 | 11 | 2 | 9 | 53 | 44 | **83.0** | 36 | 7 | 29 | 93 | 64 | **68.8** |

| **2004** | Spring cohort | | | | | | Summer cohort | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Time period | O1 | M | E | O2 | I/E# | **I/E%** | O1 | M | E | O2 | I/E# | **I/E%** |
| July25 → Aug23 | 244 | 61 | 183 | 1314 | 1130 | **86.0** | N/A | | | | | |
| Aug23 → Sept 22 | 1130 | 341 | 973 | 319 | -654 | **-67.2** | 531 | 138 | 393 | 1327 | 934 | **70.4** |
| Sept 22 → Nov 1 | 319 | 108 | 211 | 0 | -211 | **-100** | 1327 | 446 | 881 | 284 | -597 | **-67.8** |

(Table 1.12). In 2004, substantial immigration and emigration occurred and patterns were not consistent across time periods for either cohort. Immigration of the spring cohort was observed from July to August and emigration from August to September (Table 1.12). For the summer cohort, immigration was observed from August to September (Table 1.12). Emigration of both cohorts occurred from September to November, and complete emigration of the spring cohort was observed during this period (Table 1.12).

### *II. Chesapeake Bay*

Hatch date distributions in the Chesapeake Bay were bimodal in 2003 and 2004 (Fig. 1.7). Distinct temporal gaps ($\geq$ 2 weeks) were present between hatch date modes each year, which facilitated identification of seasonal cohorts (Table 1.10). In 2003, peak hatch dates of the spring and summer cohort were in early May and mid- to late July, respectively. In 2004, peak hatch dates of both spring (mid-April) and summer (June) cohorts were earlier than in 2003.

The spring cohort recruited to littoral habitats in the Patuxent River estuary as early as the first week of June in 2004, yet the spring cohort was not observed until late July in 2003 (Fig 1.10). Sizes and ages associated with these initial occurrences in 2004 were 59 – 72 mm and 52 – 63 days, respectively. In 2003, sizes and ages at initial occurrence were 120 – 122 mm and 79 – 93 days. The spring cohort was consistently collected in the Patuxent River from late July through mid-August in 2003, and from early June to mid-July in 2004. Modal size progression of the spring cohort was apparent in 2003, but not in 2004 when this cohort was not observed after July 15 (Fig. 1.10). The summer cohort was not observed until early October in 2003. In 2004, no summer-

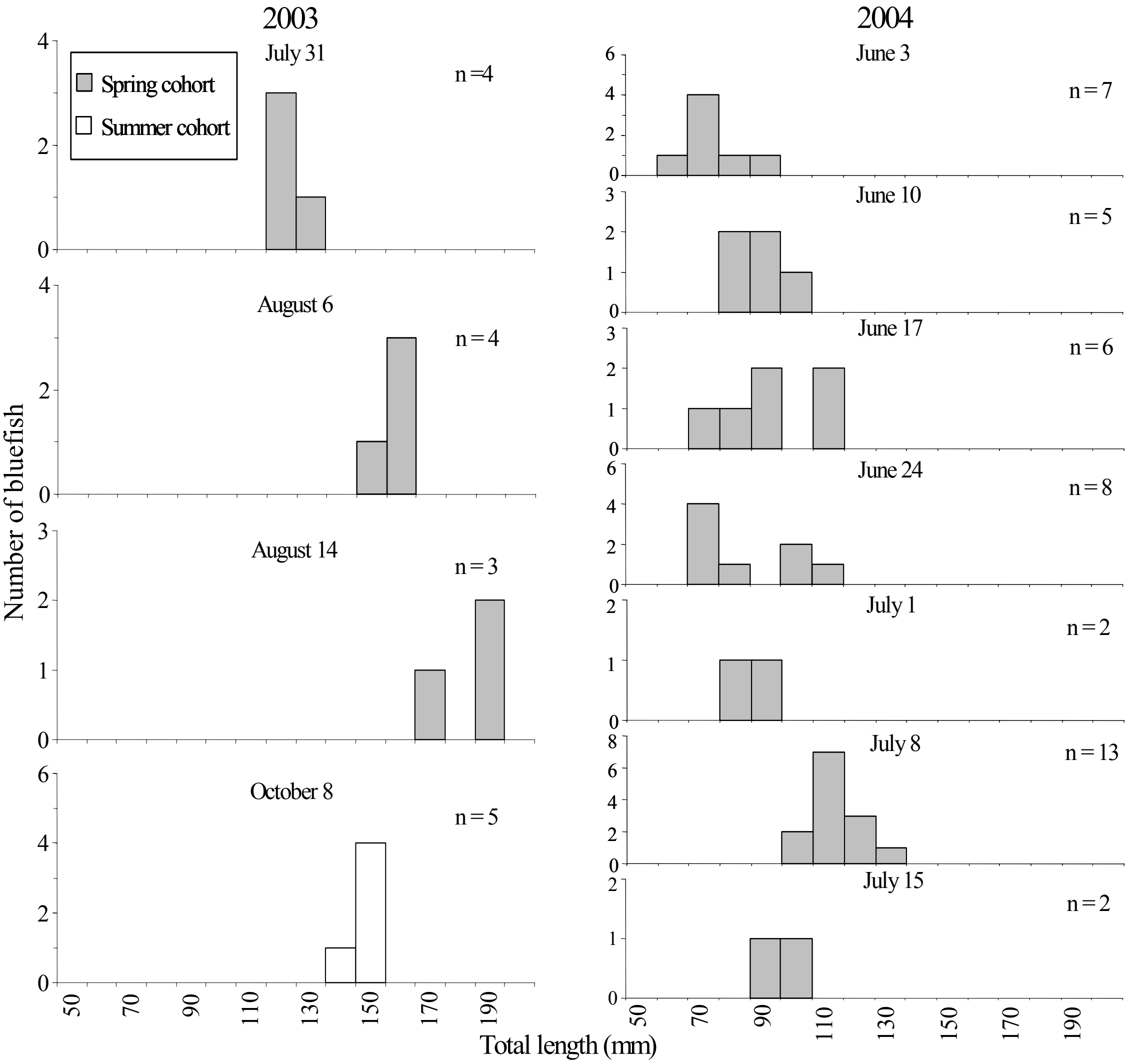


Fig 1.10. Length frequency distributions of juvenile bluefish collected at the Chesapeake Biological Laboratory site during 2003 and 2004. Weekly seining conducted from June 3 – October 8 in 2003; from May 13 to October 15 in 2004. n refers to total number of bluefish captured during each sampling event.

spawned individuals were collected in the Patuxent River at the primary sampling site (CBL pier); however, they were collected (n = 2) farther upriver on September 15. Also, the summer cohort was observed in the Nanticoke (n = 1) and Potomac Rivers (n =1) during mid-August.

### *Cohort Representation*

Correcting for cumulative mortality and inclusion of YOY larger than 200 mm increased observed frequencies of the spring cohort, and this effect appeared to be additive for coastal ocean samples, to which both modifications were made (Fig. 1.7). In the coastal ocean, relative frequencies of spring and summer cohorts did not exhibit consistent patterns across test scenarios and years. In contrast, relative frequencies of the spring cohort were consistently two to nine-fold higher than the summer cohort in Chesapeake Bay, regardless of year or test scenario (Tables 1.13, 1.14).

Relative frequencies of spring and summer cohorts were significantly different between systems in 2003 and 2004 (Tables 1.13, 1.14). In 2003, all test scenarios, except that including all YOY and not corrected for cumulative mortality, indicated the relative proportion of the summer cohort was greater than the spring cohort in coastal ocean habitats; whereas the spring cohort displayed a higher relative proportion in Chesapeake Bay (Table 1.13). In 2004, all test scenarios indicated a significant difference in relative cohort frequencies between systems. Comparisons based on frequencies that were uncorrected for cumulative mortality, irrespective of inclusion of all YOY, showed that relative cohort proportions were highest for the summer cohort in the coastal ocean and the spring cohort in Chesapeake Bay (Table 1.14). However, comparisons based on

Table 1.13. Contingency tables of frequencies of spring and summer cohorts among systems in 2003, based on calculated frequencies for each test scenario: a) YOY bluefish < 200 mm, not corrected for cumulative mortality (M); b) YOY bluefish < 200 mm and M corrected; c) All YOY bluefish, no M correction; d) All YOY bluefish and M corrected. Values in each cell are observed frequency (top), expected frequency (middle), and row percent (bottom). Chi-square tests of independence used to evaluate the null hypothesis that relative cohort frequencies were independent of system in 2003. Chi-square statistics and accompanying p-values reported; Fisher's Exact Test employed where expected frequencies < 5 for any cell.

(a) < 200 mm, no M

| System | Spring | Summer |
|---|---|---|
| Ocean | 43<br>49<br>25.1% | 128<br>122<br>74.9% |
| Ches. Bay | 10<br>4<br>66.7% | 5<br>11<br>33.3% |

Fisher's Exact Test, p = 0.002

(b) < 200 mm, M corrected

| System | Spring | Summer |
|---|---|---|
| Ocean | 71<br>83<br>34.3% | 136<br>125<br>65.7% |
| Ches. Bay | 22<br>5<br>81.5% | 5<br>14<br>18.5% |

$\chi^2 = 22.2$, $p < 0.0001$

(c) All YOY, no M

| System | Spring | Summer |
|---|---|---|
| Ocean | 97<br>100<br>43.1% | 128<br>115<br>56.9% |
| Ches. Bay | 10<br>7<br>66.7% | 5<br>8<br>33.3% |

$\chi^2 = 3.15$, $p = 0.08$

(d) All YOY, M corrected

| System | Spring | Summer |
|---|---|---|
| Ocean | 184<br>190<br>57.5% | 136<br>130<br>42.5% |
| Ches. Bay | 22<br>16<br>81.5% | 5<br>11<br>18.5% |

$\chi^2 = 5.94$, $p = 0.015$

Table 1.14. Contingency tables of frequencies of spring and summer cohorts between systems in 2004, based on calculated frequencies for each test scenario: a) YOY bluefish < 200 mm, not corrected for cumulative mortality (M); b) YOY bluefish < 200 mm and M corrected; c) All YOY bluefish, no M correction; d) All YOY bluefish and M corrected. Values in each cell are observed frequency (top), expected frequency (middle), and row percent (bottom). Chi-square tests of independence used to evaluate the null hypothesis that relative cohort frequencies were independent of system in 2004. Chi-square statistics and accompanying p-values reported.

(a) < 200 mm, no M

| System | Spring | Summer |
|---|---|---|
| Ocean | 1327<br>1357<br>40.0% | 1992<br>1962<br>60.0% |
| Ches. Bay | 55<br>25<br>88.7% | 7<br>37<br>11.3% |

$\chi^2 = 59.80$, $p < 0.0001$

(b) < 200 mm, M corrected

| System | Spring | Summer |
|---|---|---|
| Ocean | 1776<br>1839<br>45.2% | 2153<br>2090<br>54.8% |
| Ches. Bay | 126<br>63<br>94.0% | 8<br>71<br>6.0% |

$\chi^2 = 124.08$, $p < 0.0001$

(c) All YOY, no M

| System | Spring | Summer |
|---|---|---|
| Ocean | 1823<br>1849<br>45.4% | 2189<br>2163<br>54.6% |
| Ches. Bay | 55<br>29<br>88.7% | 7<br>33<br>11.3% |

$\chi^2 = 46.00$, $p < 0.0001$

(d) All YOY, M corrected

| System | Spring | Summer |
|---|---|---|
| Ocean | 2541<br>2597<br>50.9% | 2455<br>2399<br>49.1% |
| Ches. Bay | 126<br>70<br>94.0% | 8<br>64<br>6.0% |

$\chi^2 = 97.43$, $p < 0.0001$

frequencies that were adjusted for cumulative mortality indicated relative cohort proportions were approximately equal in the coastal ocean, but remained higher (~90%) for the spring cohort in Chesapeake Bay (Table 1.14).

Differences in relative cohort frequencies between years in the coastal ocean were significant for all test scenarios except that including all YOY and not adjusted for cumulative mortality, where the summer cohort exhibited similar relative frequencies (c. 55% both years) (Table 1.15). Based on cohort frequencies of YOY $\leq$ 200 mm, irrespective of whether cumulative mortality was adjusted, relative cohort proportions were higher for the summer than spring cohort in both 2003 and 2004, yet contributions of the summer cohort were greater in 2003 (65-75%) than 2004 (55-60%). Based on cohort frequencies of all YOY and corrected for cumulative mortality, relative cohort proportions were slightly higher for the spring cohort in 2003 (58%) and c. equal in 2004.

In Chesapeake Bay, differences in relative cohort frequencies between years were significant (Tables 1.16). The spring cohort dominated across years, irrespective of test scenario. In 2004, relative cohort proportions were consistently 9:1 (spring:summer), regardless of correcting for cumulative mortality (Table 1.16).

### *Growth Rates*

Cohort growth rates of juvenile bluefish ranged from 1.4 to 2.4 mm $d^{-1}$ (Fig. 1.11). All cohort-specific regressions of length-at-age were significant across year and system combinations ($p < 0.01$). In the coastal ocean during 2004, the average growth rate of the summer cohort (2.39 mm $d^{-1}$) was significantly higher v. the spring cohort (1.95 mm $d^{-1}$) (ANCOVA, $p = 0.03$). In 2003, the growth rate of the summer cohort

Table 1.15. Contingency tables of frequencies of spring and summer cohorts between years in Maryland coastal waters, based on calculated frequencies for each test scenario: a) YOY bluefish < 200 mm, not corrected for cumulative mortality (M); b) YOY bluefish < 200 mm and M corrected; c) All YOY bluefish, no M correction; d) All YOY bluefish and M corrected. Values in each cell are observed frequency (top), expected frequency (middle), and row percent (bottom). Chi-square tests of independence used to evaluate the null hypothesis that relative cohort frequencies in the coastal ocean were independent of year. Chi-square statistics and accompanying p-values reported.

(a) < 200 mm, no M

| Year | Spring | Summer |
|---|---|---|
| 2003 | 43<br>67<br>25.1% | 128<br>104<br>74.9% |
| 2004 | 1327<br>1303<br>40.0% | 1992<br>2016<br>60.0% |

$\chi^2 = 15.01$, p = 0.0001

(b) < 200 mm, M corrected

| Year | Spring | Summer |
|---|---|---|
| 2003 | 71<br>92<br>34.3% | 136<br>115<br>65.7% |
| 2004 | 1776<br>1755<br>45.2% | 2153<br>2174<br>54.8% |

$\chi^2 = 9.46$, p = 0.002

(c) All YOY, no M

| Year | Spring | Summer |
|---|---|---|
| 2003 | 97<br>102<br>43.1% | 128<br>123<br>56.9% |
| 2004 | 1823<br>1818<br>45.4% | 2189<br>2194<br>54.6% |

$\chi^2 = 0.47$, p = 0.5

(d) All YOY, M corrected

| Year | Spring | Summer |
|---|---|---|
| 2003 | 184<br>164<br>57.5% | 136<br>156<br>42.5 |
| 2004 | 2541<br>2561<br>50.9% | 2455<br>2435<br>49.1% |

$\chi^2 = 5.31$, p = 0.02

Table 1.16. Contingency tables of frequencies of spring and summer cohorts among years in Chesapeake Bay, based on calculated frequencies for the test scenarios: a) YOY bluefish < 200 mm, not corrected for cumulative mortality (M); b) YOY bluefish < 200 mm and M corrected. No YOY bluefish > 200 mm TL were observed in Chesapeake Bay in either year, hence no all YOY scenario is presented as above. Chi-square tests of independence used to evaluate the null hypothesis that relative cohort frequencies in Chesapeake Bay were independent of year. Chi-square statistics and accompanying p-values reported; Fisher's Exact Test employed where expected frequencies < 5 for any cell.

(a) < 200 mm, no M

| Year | Spring | Summer |
|---|---|---|
| 2003 | 10<br>13<br>66.7% | 5<br>2<br>33.3% |
| 2004 | 55<br>52<br>88.7% | 7<br>10<br>11.3% |

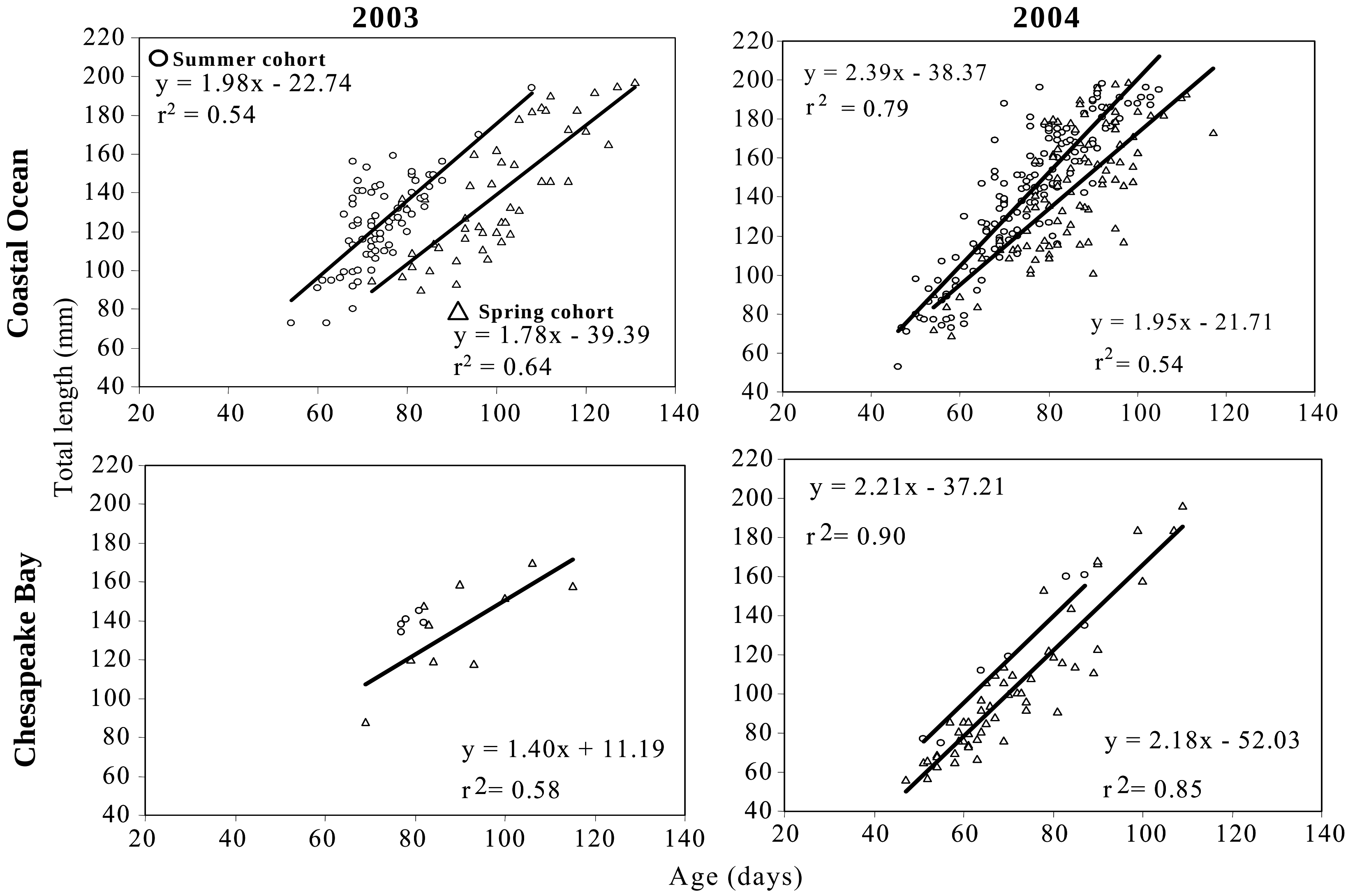
Fisher's Exact Test, p = 0.0001

(b) < 200 mm, M corrected

| Year | Spring | Summer |
|---|---|---|
| 2003 | 22<br>25<br>81.5% | 5<br>2<br>18.5% |
| 2004 | 126<br>123<br>94.0% | 8<br>11<br>6.0% |

Fisher's Exact Test, p = 0.0068

Figure 1.11. Size-at-age for juvenile bluefish cohorts in Maryland coastal waters and Chesapeake Bay across 2003 and 2004. Summer cohort denoted by circles, and the spring cohort, triangles. Least-squares linear regression used to estimate cohort growth rates.



(1.98 mm $d^{-1}$) was higher than the spring cohort (1.78 mm $d^{-1}$), yet this difference was not significant. However, the summer cohort was significantly larger at age than the spring cohort based upon differences in intercepts ($p < 0.0001$) (Fig. 1.11). In Chesapeake Bay during 2004, the growth rate of the summer cohort (2.2 mm $d^{-1}$) was almost identical to that for the spring cohort (2.18 mm $d^{-1}$); the summer cohort was significantly larger at age v. the spring cohort ($p = 0.0018$). In 2003, growth rates were not compared between cohorts because low sample size of the summer cohort (n=5) precluded estimation of growth rate for this cohort.

Growth rates of respective cohorts were not significantly different between systems. Summer-spawned juveniles inhabiting Maryland coastal waters (2004) displayed the highest observed growth rates, 2.39 mm $d^{-1}$ (Fig. 1.11). Cohort growth rates were generally higher in 2004 (1.95 – 2.39 mm $d^{-1}$) than 2003 (1.40 – 1.98 mm $d^{-1}$) (Fig. 1.11), although differences were not significant.

## Discussion

This study demonstrated that juvenile bluefish recruit to and utilize coastal ocean habitats as nurseries in addition to estuaries. Hatch dates of recruits in Maryland coastal waters were broadly similar between years, peaking in spring (April – May) and summer (July), yet specific recruitment patterns differed between years. Bimodal recruitment was observed during 2003, but in 2004 hatch date distributions were continuous and distinct “spring” and “summer” cohorts were less evident. A bimodal recruitment pattern was observed in Chesapeake Bay for both years. Interestingly, peaks of respective hatch modes coincided between systems in 2003; whereas in 2004, cohort hatch peaks in the coastal ocean lagged c. 1 month behind those in Chesapeake Bay. In fact, across systems, hatch dates of recruits in 2004 spanned from early March to mid-August, with no temporal gaps in hatch dates (Fig. 1.7). These results suggest bluefish spawning is not strictly pulsed and that recruitment patterns show significant interannual variations within and between oceanic and estuarine nursery habitats.

Still, between systems there were consistent amplitudinal differences in cohort representation. The spring cohort dominated in Chesapeake Bay both years, whereas in coastal ocean habitats, the summer cohort was consistently abundant, either of greater (2003) or similar (2004) abundance to the spring cohort. Also, patterns of relative cohort contribution in the coastal ocean were dependent on test scenario (i.e., inclusion of larger YOY and/or a cumulative mortality correction). Growth rates of juvenile bluefish inhabiting Maryland coastal waters were rapid, ranging from 1.8 – 2.4 mm $d^{-1}$. Average growth rates of the summer cohort were higher than the spring cohort, and significantly so in 2004, supporting my hypothesis that summer-spawned bluefish exhibit higher growth rates than spring-spawned bluefish in coastal ocean habitats (data was insufficient to permit comparison of summer v. spring cohort growth in Chesapeake Bay). Although no significant differences were found in growth rates of juveniles between nursery habitats, growth rates were equivalent or higher for respective bluefish cohorts in Maryland coastal waters compared to Chesapeake Bay.

## *Recruitment dynamics of bluefish in Maryland's coastal ocean environment*

### *Hatch Dates in Relation to Bluefish Spawning*

Hatch dates of bluefish recruits in 2003 were clearly bimodal, peaking in April and July, with a prominent gap (June) in hatch dates between these two modes. Conversely, the hatch date distribution in 2004 was more continuous; although two peaks (early May and early July) were observed, there was no temporal gap in hatch dates. Previous studies investigating bluefish recruitment to estuarine habitats have found bimodal hatch date distributions, with peaks in April and July, and a persistent absence of recruits with hatch dates from late May to June (Nyman and Conover 1988; McBride et al. 1991; McBride et al. 1993). These investigators attributed the paucity of early summer (late May – June) recruits to a lack of spawning during this period. Yet, Hare and Cowen (1993) and Smith et al. (1994) analyzed data from synoptic ichthyoplankton collections and proposed that spawning was indeed protracted, and suggested that the appearance of a bimodal pattern of hatch dates could be generated by either low probability of survival for offspring produced during early summer (due to unfavorable transport) or recruitment of these individuals to habitats/regions where hatch dates have not been documented. My results lend support to the "continuous-spawning" hypothesis of Hare and Cowen (1993) and Smith et al. (1994). Juveniles with hatch dates during this "gap" period, late May – June, were common in Maryland coastal waters during 2004; hence, some spawning occurs during this period. Further, it seems likely that these early summer offspring may primarily recruit to shallow coastal environments.

Bluefish undertake extensive seasonal spawning migrations, and initial spatiotemporal placement of eggs and subsequent transport of larvae has important consequences for the magnitude and timing of recruitment to particular regions or nursery habitats. Peak hatch dates of recruits in Maryland coastal waters were generally in the spring (March-April) and summer (July) across years. These recruits are likely products of the major spawning events in the SAB during spring (March-May) and MAB during summer (July). Spring-spawned offspring can potentially colonize nursery habitats along MAB and SAB regions of the U.S. East coast (McBride et al. 1993). The epicenter of summer-spawning consistently occurs in mid-shelf waters off the coast of New Jersey and southward to Delaware Bay (Smith et al. 1994). Given our sampling region is only 50 – 100 km southward of this spawning concentration, and the general southward along-shore flow (5 – 10 cm $s^{-1}$) of surface waters in the MAB during summer (Epifanio and Garvine 2001), the observation of consistently high abundances, in both 2003 and 2004, of summer-spawned bluefish is not surprising. What is intriguing though is the finding that recruits with early summer (June) hatch dates were common in 2004, but rare in 2003.

Bluefish are believed to migrate northward from the SAB to the MAB during late May or June. Investigators observed eggs and larvae in June from Cape Hatteras to southern New Jersey, with highest concentrations in mid-shelf waters in the southern MAB (Virginia and North Carolina, north of Cape Hatteras) (Norcross et al. 1974; Smith et al. 1994). Accordingly, transport of pelagic larvae, and subsequent recruitment of juveniles (aided by wind-driven Ekman transport) to nurseries, should occur southward of production areas (i.e., south of Delaware Bay). Previous studies that have documented a persistent temporal gap in hatch dates from late May through June (Nyman and Conover 1988; McBride and Conover 1991) were focused in regions of the northern MAB, northward of production areas, where low recruitment probability of June progeny would be expected (*sensu* Smith et al. 1994). Conversely, the appearance of June progeny in our sampling domain appears feasible.

Although spawning activity in June appears concentrated in the southern MAB, high egg densities (101 – 1000 $m^{-2}$) have been reported off Delaware Bay (Smith et al. 1994), just proximately north of our sampling region. Hare and Cowen (1993) proposed that larvae from spawning in the southern MAB are swept southward in along-shore currents and become entrained in the Gulf Stream, after which they must cross the Slope Sea and traverse the shelf if they were to recruit to nurseries. However, their transport model predicted low recruitment probabilities of these offspring. Bumpus (1969) showed that surface flows in the MAB could shift during summer and maintain a reverse direction (i.e., north vs. south) over time scales of weeks when low runoff from Delaware and Chesapeake Bays was coupled with strong southerly winds. This flow regime would carry larvae northward, reducing their chances of being entrained in the Gulf Stream and/or enhancing local recruitment. However, this did not appear to be a plausible mechanism based upon wind data from NOAA Buoy #44014, ~64 nautical miles (nm) off Virginia Beach. These records indicated June winds were predominantly to the south (i.e., north winds) during both years of this study.

Norcross et al. (1974) attributed interannual fluctuations in bluefish egg abundances in coastal water of Virginia and North Carolina during the month of June to temperature differences between years, where spawning appeared to be delayed in cooler years. The minimum reported water temperature for the occurrence of bluefish eggs is 18 $^{o}$C, with eggs common in waters 18 – 22 $^{o}$C (Norcross et al. 1974; Hare et al. 1999).

Daily water (surface) temperatures off the coast of Virginia (NOAA Buoy #44014) and Delaware (NOAA Buoy #44009 ~15 nm SE of Cape May, NJ) were $\geq 18\ ^{o}$C throughout June 2004, but in 2003 temperatures were either $< 18\ ^{o}$C (1-15 June: Virginia; 1-30 June: Delaware) or hovered slightly above the threshold (16-30 June: Virginia) (Fig. 1.12). Consequently, the expected window for spawning activity during June was greater in 2004 than 2003. The warmer early summer temperatures were consistent with the observed earlier hatch peak of the summer cohort in 2004 (early July) than in 2003 (late July). Takata (2004) also found evidence of early summer recruits in Maryland coastal waters during 2000 and 2001. Temperature records for these years showed June temperatures mostly above $18^{o}$ C, except for the first week of June (Fig. 1.12). Moreover, average June temperatures were significantly lower in 2003 than in all other years (Table 1.17). Hence, the paucity of June recruits observed in 2003 might be explained by low water temperatures in that year. These results suggest that bluefish spawning during June may be dependent upon suitable temperatures in shelf waters.

Another pelagic species which spawns in continental shelf waters of the Atlantic Ocean, butterfish *Peprilus triacanthus*, shares a common reproductive strategy with bluefish: spawning in the SAB during spring is followed by northward migration to the MAB for summer spawning. Interestingly, Rotunno and Cowen (1997) observed a pattern of interannual variability in hatch dates of butterfish similar to that observed in this study. Hatch date distributions in 1989 were bimodal with a temporal gap in hatch dates during the proposed northward migration (April → May), yet in the previous year, hatch dates showed two peaks but were semi-continuous, evidence that recruits were spawned during the migration period. This similarity of reproductive strategy between

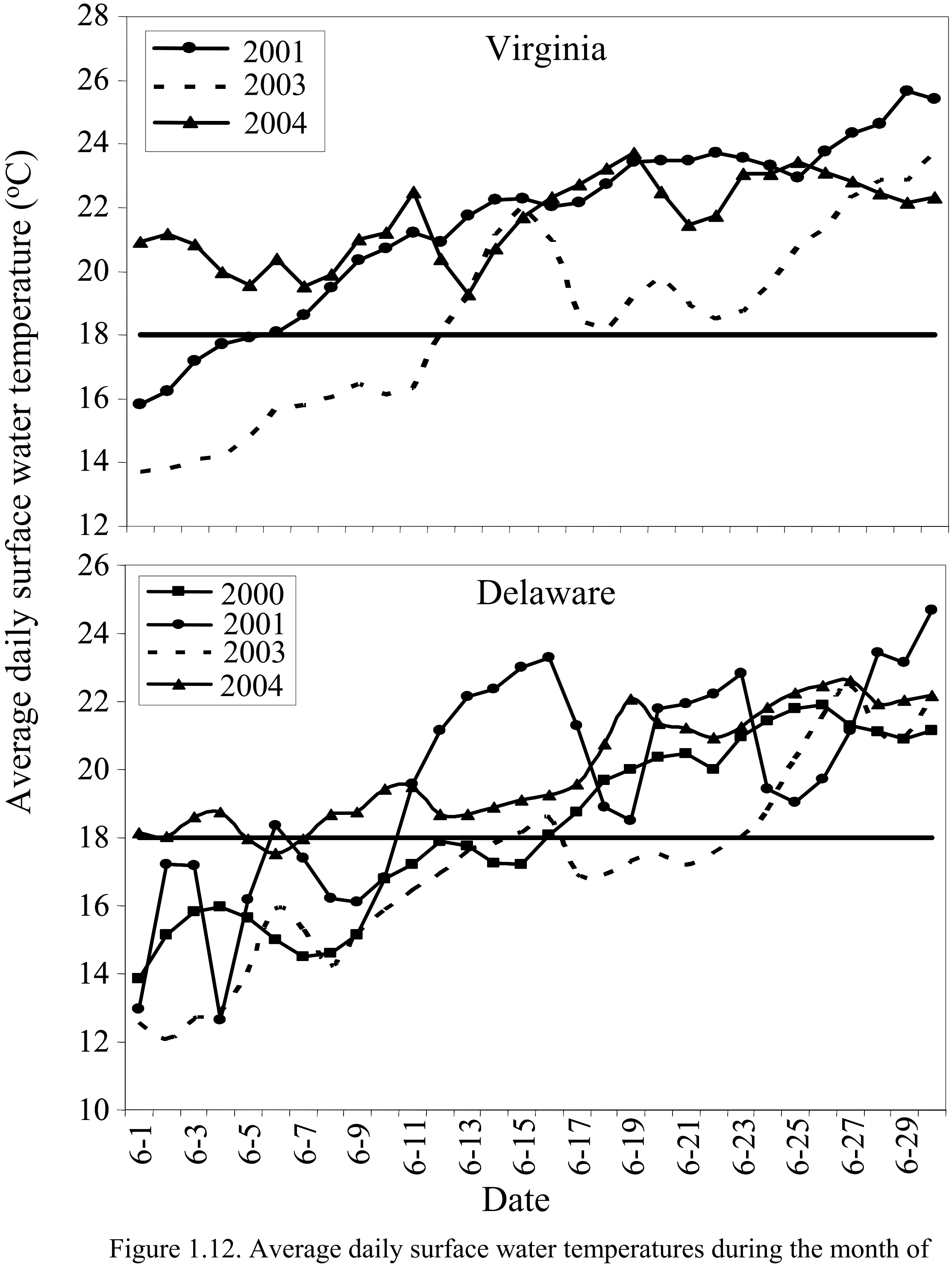


Figure 1.12. Average daily surface water temperatures during the month of June in various years in continental shelf waters off the Virginia coast (NOAA Buoy #44014) and inner shelf waters off Delaware Bay (NOAA Buoy #44009). The solid reference line at $18^{o}$ C indicates the minimum temperature at which bluefish eggs have been collected.

Table 1.17. Average June water temperatures (surface) in respective years in shelf waters off Virginia (NOAA Buoy #44014) and Delaware (NOAA Buoy #44009).

| Year | Virginia temp ($^oC$) | Delaware temp ($^oC$) |
|---|---|---|
| 2000 | N/A | 18.3 |
| 2001 | 21.5 | 19.7 |
| 2003 | 18.4 | 17.1 |
| 2004 | 21.6 | 20.0 |

these two coastal spawners implies an adaptive advantage of continuous rather than pulsed spawning.

Temporal spawning patterns of bluefish do not appear to be consistently pulsed or continuous across populations occurring in other regions of the world. In a review, Juanes et al. (1996) noted that spawning was pulsed in the Gulf of Mexico, Northwest Africa, and Western Australia; but continuous in the Black Sea, eastern coast of South America, and southeastern Africa. Evidence of spawning patterns was typically based on icthyoplankton collections (Juanes et al. 1996). Unfortunately, how pulsed or continuous spawning is related to subsequent juvenile production remains unknown in these systems; except for Northwest Africa, where both pulsed spawning and recruitment has been reported (Juanes et al. 1996).

The bimodal hatch date pattern observed in Maryland coastal waters in 2003 was preserved when hatch date estimates of larger YOY (> 200 mm) were included. Also, inclusion of hatch dates of larger YOY reinforced the continuous nature of the 2004 hatch date distribution. The approach of extrapolating the age-length relationship of YOY < 200 mm to YOY > 200 mm assumed that growth rate was constant. If larger YOY>200 mm grew at faster or slower rates than smaller YOY, their inclusion would result in over- and under-estimation of spring cohort contributions, respectively. Nyman and Conover (1988) and Creaser and Perkins (1994) showed declining growth rates at lengths greater than 150 mm fork length (FL). Calculated prediction intervals of ages of YOY > 200 mm were ± 3-4 weeks in both 2003 and 2004. Consequently, if ages were overestimated in 2003, then hatch dates would have been semi-continuous rather than bimodal. However, hatch date estimates of bluefish directly aged (≤ 200 mm) should be reflective of temporal recruitment patterns because sampling occurred throughout the entire recruitment period.

The use of different gear types between years in the coastal ocean is an important caveat in this study. The large bottom trawl we deployed in 2004 was a much more powerful and efficient gear relative to the mid-water trawl used in 2003. Although each trawl captured individuals over the size range of interest (< 300 mm), larger YOY > 200 were more prevalent, and overall catches an order of magnitude higher, in bottom trawl collections (Fig. 1.8). Additionally, sampling efforts were not homogenous across cruises in 2004. Therefore, abundances were standardized, and age-length keys were applied in conjunction with age estimation of larger YOY (> 200 mm) to yield age compositions and associated hatch dates and cohort assignments of all YOY bluefish. These extra data manipulations, not necessary for 2003 data analysis, likely resulted in 2004 hatch dates and cohort abundances with more compounded error than those in 2003.

### *Temporal Recruitment Patterns of Juveniles*

Juvenile bluefish may recruit to MAB estuaries earlier than to coastal ocean habitats. Spring-spawned juvenile bluefish were first observed in Maryland coastal waters during July in both years, at ages of 72 – 91 days and 54 – 111 days in 2003 and 2004, respectively. No YOY bluefish were observed in June of 2003 in the coastal ocean (no sampling occurred in June 2004). Takata (2004) and R. Woodland (personal communication) also noted that YOY bluefish were absent from Maryland coastal waters during mid-June in 2001 and 2005, respectively. Further, Able et al. (2003) observed very low abundances (total n = 0 – 10) of the spring cohort in coastal waters off New Jersey from mid- to late June across four years of sampling (1995-1998). The initial appearance of the spring cohort in estuaries of New York, New Jersey, Rhode Island (Nyman and Conover 1988; McBride and Conover 1991; McBride et al. 1995) and Chesapeake Bay (Takata 2004; this study) has been reported to occur as early as late May or early June. Estimated ages at first recruitment to estuaries are approximately 60 – 70 days (McBride and Conover 1991). Thus, evidence to date indicates that the spring cohort recruits earlier to MAB estuaries than to coastal ocean habitats. In selecting initial nursery habitats, YOY may select warmer late spring habitats, which occurred in shallow estuarine (18 – 22$^{o}$ C) v. coastal ocean (15 – 16$^{o}$ C) habitats from May – June in both 2003 and 2004 (Fig. 1.13).

The small sizes and early ages of summer-spawned juveniles suggest these individuals initially recruited to the coastal ocean environment. Summer-spawned juvenile bluefish were first observed in Maryland coastal waters during late September in 2003 and late August in 2004. The earliest ages and smallest sizes of the summer cohort were 46 to 85 days and 55 to 150 mm across years. These estimates were generally lower than those for the spring cohort in coastal habitats, but were similar for estuarine arrival ages/sizes for: Chesapeake Bay summer (51 – 55 days; 77 – 79 m TL) and spring cohorts (52 – 63 days; 59 - 72 mm TL), and New York estuaries for spring (60 – 68 d; 30 – 65 mm FL) (McBride and Conover 1991; Nyman and Conover 1988) and summer cohorts (40 – 60 days; 46 – 60 mm FL) (McBride and Conover 1991).

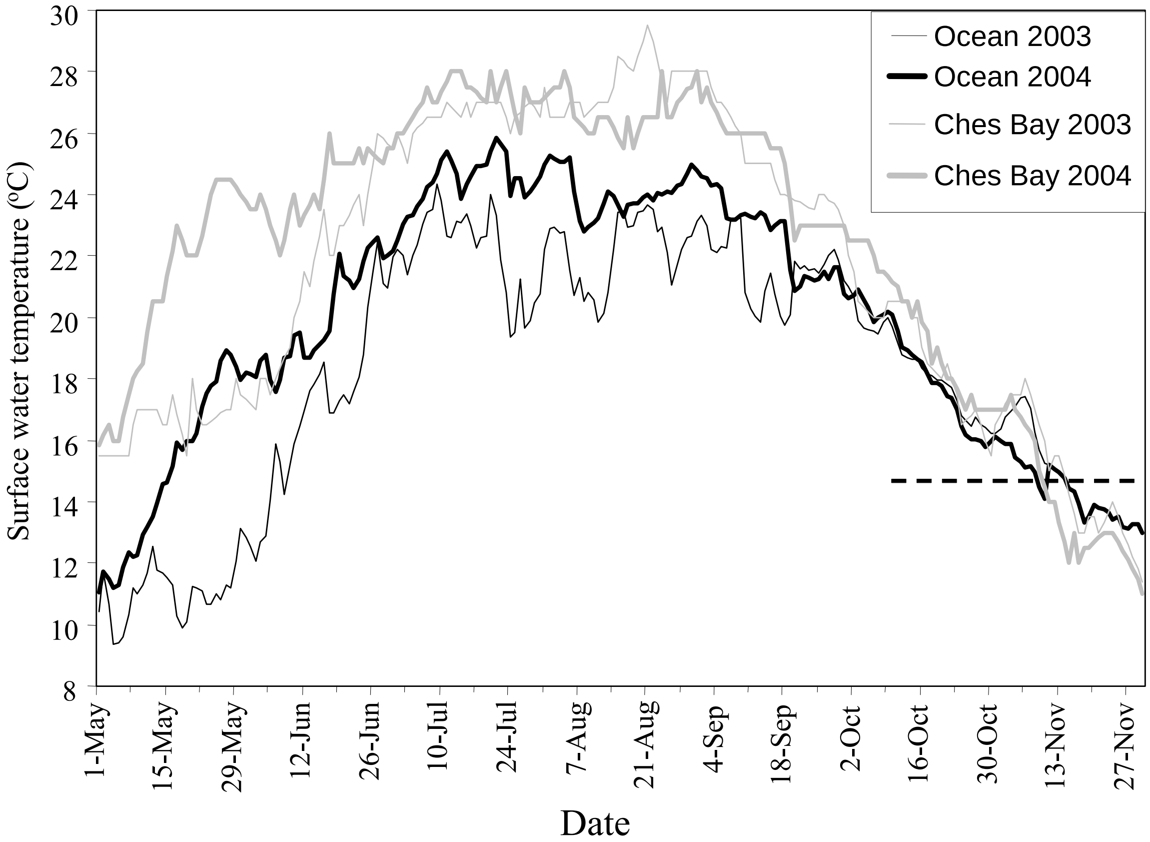


Figure 1.13. Daily surface water temperatures from May through late November in inner shelf waters off Delaware Bay (NOAA Buoy #44009, a surrogate for temperature trends at our coastal sampling region, see text) and Chesapeake Bay (Chesapeake Biological Laboratory site) in 2003 and 2004. Black lines represent coastal ocean; gray lines Chesapeake Bay. Thicker, bolded lines show 2004 temperatures; thinner lines 2003 temperatures. Dashed reference line depicts average reported temperature (15 $^{o}$C) for triggering fall emigration of YOY from estuaries/coastal waters

### *Cohort Representation*

Relative cohort contributions to juvenile bluefish abundance in the coastal ocean were slightly higher for the spring cohort in 2003 but approximately equal in 2004. However, uncertainties regarding residency, possible emigration from estuaries, and size distinctions between YOY and yearling bluefish may confound interpretations of relative cohort frequencies. In 2003, the relative contribution of the spring cohort was greatest (58%) when hatch date frequencies of all YOY (incorporating YOY > 200 mm) were considered and frequencies were corrected for cumulative mortality. However, of the 54 larger YOY collected in 2003, 50 (93%) of these fish were collected in October, during which I found evidence of substantial emigration of spring-spawned individuals from outside areas into our study area (Table 1.12). Conceivably most or all spring-spawned fish > 200 mm observed in October, which I classified as immigrants (n = 44, based on immigration/emigration estimates) could represent individuals emigrating from estuarine habitats to our sampling region v. originating from other coastal regions. Under this scenario, adjusting for this bias could reduce, by half, the actual contribution of spring-spawned bluefish in 2003 (i.e., these individuals do not utilize the coastal ocean). Cohort frequencies based on only on YOY $\leq$ 200 mm, and corrected for cumulative mortality showed decreased contributions of the spring cohort (34%), with the summer cohort dominating (66%).

In 2004, substantial immigration/emigration (Table 1.12) and non-overlapping hatch modes among months of the spring cohort suggested that this cohort was transient in the sampled region of the coastal ocean. Therefore, estimates of the contribution of this cohort undoubtedly contained errors, as cohort frequencies were summed across all sampling events. The fact that no clear division existed between seasonal cohorts in 2004 further complicated evaluation of relative cohort contributions in 2004 (i.e., cohort designations were somewhat arbitrary). Yet, the observed nadir in hatch date distributions was used as the division between seasonal cohorts; which resulted in similar cohort definitions as those in 2003. Additionally, the more efficient gear employed in 2004 v. 2003 and uncertainties concerning monthly maximum sizes of YOY may have led to an overestimation of contribution of spring-spawned YOY. In summary, although there was no single test scenario representing the most parsimonious contrast of relative cohort frequencies in 2004, it appears the relative frequencies of cohorts were approximately equal, although the summer cohort seemed to exhibit a higher degree of residency than the spring cohort (see below and Table 1.12).

Other investigators have noted the presence of both spring and summer-spawned juvenile bluefish in coastal ocean environments during summer. Able et al. (2003) found both spring and summer-spawned juveniles were present in coastal ocean environments of New Jersey from July – October. Based on presumed cohort sizes, these authors concluded the abundance of the summer cohort was higher and more consistent than the spring cohort. Also, McBride et al. (1993) noted the occurrence of spring-spawned juveniles (direct ageing) off the coast of North and South Carolina during July. Therefore, it appears that both spring and summer cohorts utilize coastal ocean habitats. Taken together with my analysis, evidence suggests that coastal ocean habitats may function as a vital nursery habitat for the summer cohort, but as a corridor or opportunistic habitat for the spring cohort. The spring cohort probably relies mostly on estuaries as nurseries relative to coastal ocean habitats. In this regard, Neuman and Able

(2003) found macro-scale habitat use differed between seasonal cohorts of another estuarine, coastal fish, the windowpane, *Schopthalamus aquosus*, whereby the spring cohort primarily settled in estuarine habitats and the fall cohort settled exclusively in coastal ocean habitats.

The spring cohort dominated in the Chesapeake Bay, albeit at relatively low abundances compared to other estuarine systems. Mean annual relative abundances of the spring cohort (0.6 – 1.4 per seine haul) (Chapter 2) were similar to those reported from New Jersey estuaries (0.2 – 1.1 haul$^{-1}$), but somewhat lower than in New York estuaries (2.6 – 3.2 haul$^{-1}$) (McBride and Conover 1991). Also, McBride et al. 1995 observed that mean annual relative abundance in Narragansett Bay, RI ranged from 1.4 – 12.9 haul$^{-1}$ (geometric v. arithmetic mean) from 1986 - 1992; meanwhile bay-wide YOY abundance (also geometric mean per haul) in littoral habitats Chesapeake Bay (July – September, irrespective of cohort) was much lower during the same period (0.06 – 0.22 haul$^{-1}$). Therefore, it appears that although the Chesapeake Bay estuary is utilized by the spring cohort, more northerly estuaries of the MAB may be more important nurseries.

### *Immigration and Emigration from Coastal Ocean Habitats*

Juvenile bluefish are highly mobile, cruising predators that are capable of sustained swimming speeds of 26 cm s$^{-1}$ (Olla et al. 1985); therefore they have the capacity to undergo extensive (10 – 100 km) movements over relatively short time periods (e.g., days to months). A major assumption in this study was that YOY bluefish use coastal ocean environments as a resident, as opposed to a corridor habitat. If the latter were true, then bluefish captured in coastal ocean habitats could represent individuals that have recently exited or are about to enter estuaries or YOY that move into and out of the sampled coastal ocean habitats from adjacent ones not sampled. If juvenile bluefish do not use the coastal ocean as a resident habitat or habitat use varies between cohorts, this would bias cohort contribution comparisons between nursery systems or between cohorts within a system among years. The presence of "non-resident" or transient individuals would artificially inflate their contribution in the coastal ocean. Furthermore, growth rates might be confounded (see below), as estimated oceanic growth rates would not fully represent residency in regional oceanic habitats.

Other investigators have provided positive (albeit limited) evidence of coastal residency patterns. Able et al. (2003) found no evidence of exchange of tagged (coded wire tags) YOY bluefish between oceanic and estuarine habitats of New Jersey; however, only 2 of 5636 individuals (<0.04%) tagged on ocean beaches were recaptured. Takata (2004) employed otolith microchemistry techniques (Sr:Ca ratios of life history transects) to evaluate habitat utilization of juvenile bluefish in Chesapeake Bay and Maryland coastal waters. Her study indicated that all summer-spawned bluefish captured in Maryland coastal waters had remained resident in the coastal ocean throughout summer and early fall; the majority of YOY (both cohorts) collected in Chesapeake Bay exhibited Sr:Ca values indicative of estuarine residency.

In 2003, some spring-spawned individuals appeared to remain in coastal ocean habitats during summer; considerable immigration of both spring and summer cohorts to our sampling region occurred during fall (October), likely due to southward coastal migration of juveniles from more northern regions. Immigration of the spring cohort was minimal from July through September, and was largest from early to late July (Table 1.12), likely resulting from the arrival of spring-spawned YOY sometime between our

July sampling events, as individuals of ages 60 – 70 days (i.e., recent recruits) were common in late July. Minimal immigration/emigration and largely overlapping hatch dates (Fig. 1.9) of the spring cohort across July → September suggests a degree of residency of this cohort. Surface temperatures during October 2003 within our region were c. 19 $^{o}$C, four degrees higher than the reported threshold temperature for triggering fall migration (Lund and Maltezos 1970). Accordingly, the substantial immigration of both cohorts observed from late September to October was likely a result of juveniles emigrating southward from more northern nursery habitats, which experience cooler temperatures earlier in the fall. For instance, absence of YOY bluefish in estuaries has been reported to occur in Maine during mid-September (Creaser and Perkins 1994), early October in Rhode Island (McBride et al. 1995), and mid-October in New York (Nyman and Conover 1988).

In 2004, the spring cohort exhibited significant immigration/emigration (not consistently one or the other) across months (Table 1.12). Substantial immigration was observed from July to August, followed by large emigration from August to September. Moreover, hatch modes of the spring cohort shifted substantially among months. In July, bluefish with April hatch dates were common, yet in August, the observed hatch peak was c. 1 month later and individuals with April hatch dates were rare. Although the modal progression of hatch modes among months could be due to mortality, mortality would have to be "inverse size-selective", with a greater mortality rate for older, larger individuals v. smaller, younger individuals to generate such a progression. Typically, smaller fish experience higher mortality than their larger conspecifics (Peterson and Wroblewski 1984; Sogard 1997). This pattern of considerable immigration and emigration associated with hatch date progressions might suggest that the ocean functions as a “corridor habitat” for spring-spawned bluefish, whereby our fixed sampling domain receives new recruits from a continuous offshore larval pool (i.e, continuous spawning) and we are essentially sampling the spring cohort *en route* to estuaries or other coastal ocean regions.

In contrast, immigration/emigration estimates and hatch date patterns for the summer cohort in 2004 provided some evidence of residency of this cohort. For instance, large immigration from August to September was likely a result of new summer-spawned recruits to our region between sampling events. Interestingly, the lower range of hatch modes of the summer cohort remained stable and large shifts in hatch modes across months were not observed (Fig. 1.9), in contrast to the spring cohort, suggesting a higher degree residency of the summer than the spring cohort in coastal ocean habitats. Substantial emigration of both cohorts was observed from September to November, indicative of emigration southward as average water temperature declined below 16 $^{o}$C (Fig. 1.13), the threshold for fall emigration.

### *Recruitment Dynamics of Bluefish in Maryland’s Chesapeake Bay*

The spring cohort dominated over the summer cohort in Chesapeake Bay. Hatch dates distributions in 2004 were very similar to those analyzed by Takata (2004) for Chesapeake Bay during years 1999 to 2001, whereby hatch date distributions were largely bimodal, with the peak hatch mode occurring in April. Interestingly, means of respective modal hatch dates fell within the same week among all four years analyzed

(1999-2001, 2004), suggesting that recruitment to Chesapeake Bay may occur by similar mechanisms across years.

Early spring recruits to Chesapeake Bay probably originate from the same spawning period and location (SAB) as do spring recruits in Maryland coastal waters. A major difference, though, is that Chesapeake juveniles migrate through the coastal-estuarine ecotone some 150 km south of our sampling region. Takata (2004) suggested that the behavior of the Chesapeake Bay plume and associated outflow events may influence entry of small juveniles, with high flow events hindering entry. The presence of recruits with March hatch dates in Chesapeake Bay and their absence in the coastal ocean, and the earlier modal spring hatch date peak for Chesapeake Bay cohorts supports the view that YOY spawned early in spring primarily recruit to MAB estuaries rather than coastal ocean environments. Further, the observed temporal gap in the 2004 Chesapeake Bay hatch date distribution (late May) was apparently not due to lack of spawning activity, because this period coincided with peak hatch dates in the nearby coastal ocean region during the same year.

The lack of June recruits to Chesapeake Bay in 2003 was unusual compared to other years. This may have resulted from sampling error associated with a low sample size (n = 15) and restricted sampling domain during this year. Samples were only collected at the CBL pier in 2003; in contrast samples were obtained from throughout Maryland's portion of Chesapeake Bay in 2004 (n=62) and 1999-2001. On the other hand, it is noteworthy that the lack of June recruits in comparison to other years (1999-2001, 2004) coincided with the low temperatures during April and May in shelf waters off Delaware and Virginia (Fig. 1.12).

Summer cohort bluefish (i.e., hatch dates after June) are rare in Chesapeake Bay. Juveniles with July hatch dates were present in Chesapeake Bay during 2003, albeit at low numbers (n = 5). Takata (2004) estimated historical recruitment patterns in Chesapeake Bay, based upon length data supplied from a MD state monitoring program. She observed that summer-spawned bluefish were virtually absent from 1962 to 1999. This finding is probably related to spawning location and larval transport. Although eggs have been collected off the mouth of the Chesapeake Bay during July, spawning in July is concentrated in the northern part of the MAB (e.g., NJ waters) (Smith et al. 1994), distant from the Chesapeake Bay. Therefore, a larval and/or YOY bluefish hatched during July in shelf waters would have to undergo extensive and possibly energetic taxing migration southward to reach the mouth of Chesapeake Bay. The tradeoff between migration and growth may favor coastal inhabitance for summer cohort YOY as prey densities (Chapter 2) and temperatures become increasingly favorable as summer progresses. Interestingly, in regions where recruitment potential of summer-spawned bluefish to estuarine habitats is likely higher than in Chesapeake Bay (e.g., New Jersey, New York), investigators have found the spring cohort still dominates across years (Nyman and Conover 1988; McBride and Conover 1991; Creaser and Perkins 1994; McBride et al. 1995). In these systems, recruitment of summer-spawned individuals was sporadic across years and studies. These findings, in addition to the relatively high abundances of summer-spawned juveniles we observed in the coastal ocean environment, lend further support to my hypothesis that the spring cohort primarily utilizes estuarine habitats as nurseries, while the summer cohort dominates in coastal ocean habitats.

### *Juvenile Growth Rates in Maryland's Coastal and Estuarine Habitats*

Juvenile bluefish experience rapid growth rates in coastal ocean, as well as estuarine environments. Cohort growth rates were similar or higher, although not significantly so, in coastal ocean v. Chesapeake Bay habitats (Fig. 1.11). Water temperatures alone did not seem to explain system trends in growth rates. During the period when the spring cohort was present in each system, water temperatures were c. $4^{o}$ higher in Chesapeake Bay than Maryland coastal waters (Fig. 1.13). Although growth rates of the spring cohort were marginally higher in warmer estuarine habitats in 2004, growth of the spring cohort was somewhat higher in the coastal ocean in 2003. My growth rate estimates for juveniles inhabiting coastal ocean environments are among the highest reported for YOY bluefish (Table 1.18). Because most estimates come from estuarine habitats, this suggests that coastal ocean habitats may support higher or similar growth rates than estuarine habitats.

Within coastal ocean environments, summer-spawned bluefish seem to exhibit higher growth rates than spring-spawned individuals. Very rapid growth of the summer cohort, 2.39 mm $d^{-1}$, was observed in 2004. Again, water temperatures did not seem to explain differences in growth rates. Water temperatures were c. 3 $^{o}$C higher from July – late August (when the spring cohort was observed) than late August – October (when the summer cohort was observed) across years (Fig. 1.13), yet growth rates were higher for the summer cohort. Prey availability also influences growth rates; higher growth rates of the summer cohort may be related to elevated abundances of principal prey, YOY bay anchovy, during late summer (see Chapter 2). Takata (2004) also observed very high growth rates, 2.63 mm $d^{-1}$, for the summer cohort in Maryland coastal waters in 2000.

Table 1.18. Reported field growth rates of juvenile bluefish.

| Region | Habitat | Growth Rate (mm $d^{-1}$) | Study |
|---|---|---|---|
| MD | Ocean | 1.78 – 2.39 | This study |
| MD | Ocean | 1.45 – 2.63 | Takata 2004 |
| NJ | Ocean | 0.8 – 1.4 | Able et al. 2003 |
| MD | Estuary | 1.4 – 2.21 | This study |
| MD | Estuary | 2.03 – 2.49 | Takata 2004 |
| ME | Estuary | 0.7 – 1.31 | Creaser and Perkins 1994 |
| RI | Estuary | 0.9 – 2.1 | McBride et al. 1995 |
| NY-NJ | Estuary | 0.8 -1.44 | McBride and Conover 1991 |
| NY-NJ | Estuary | 1.3 | Nyman and Conover 1988 |
| NJ | Estuary | 0.2 – 2.2 | Able et al. 2003 |
| NC-SC | Estuary | 1.2 – 1.86 | McBride et al. 1993 |

Where differences between cohort growth rates were not significant, the summer cohort was still consistently larger at age than the spring cohort (coastal ocean 2003; Chesapeake Bay 2004). McBride and Conover (1991) and Takata (2004) also found this pattern. McBride and Conover (1991) found that growth rates during pre-recruitment phases (i.e., average growth rate before the initial appearance of respective cohorts) were significantly higher for the summer than the spring cohort and attributed this difference to warmer water temperatures during larval transport of the summer cohort. They concluded that while growth rates between cohorts *during* the juvenile period may be similar, the summer cohort remains larger at age because of larger sizes at initial recruitment to nursery habitats.

Due to rapid growth rates, the summer cohort is capable of attaining relatively large sizes by the end of the growing season, which has important implications in assessment of relative cohort contributions to the adult stock. Previous studies have concluded the adult population is comprised mostly of spring-spawned bluefish because back-calculated sizes at age 1 were unimodal, with sizes corresponding to those expected for spring-spawned juveniles: ranging from 200 – 300 mm fork length (FL) and peaking at sizes 250 mm FL (Chiarella and Conover 1990; Conover et al. 2003). Further, these authors concluded that if summer-spawned individuals were to contribute to the adult population, two size modes should be evident, because recruitment appeared strictly bimodal (bimodal hatch dates and size distributions in early fall, corresponding to spring and summer cohorts).

My results and those of Takata (2004) indicate rapid growth of summer-spawned bluefish (2.0 - 2.6 mm $d^{-1}$) in coastal ocean environments; in 2004, summer cohort bluefish attained lengths of 180 mm FL as early as September. Further, length distributions during fall were bimodal each year (Fig. 1.8), yet all bluefish in November 2004 were summer-spawned individuals (Fig. 1.9); assuming age estimation methods for YOY larger than 200 mm were valid (see above), summer-spawned bluefish appeared to reach lengths of 200 – 300 mm TL (180 – 270 mm FL) by early November. In 2004, if the traditional size threshold between cohorts during fall (200 mm FL) was employed to identify cohorts, half of the YOY would be mistakenly classified as the spring cohort. Therefore, it seems possible that previously reported, back-calculated lengths at age 1 of 200 – 300 mm FL may represent a mixture of summer- and spring-spawned bluefish, rather than exclusively the latter. For example, a bluefish hatched on July 15, experiencing larval growth of 0.5 mm $d^{-1}$ (Hare and Cowen 1994) and juvenile growth of 2.4 mm $d^{-1}$ would be 210 mm TL or 190 mm FL by November 1. Given that annulus formation is thought to occur sometime in May (Terceiro et al. 1993), and some growth must occur between early fall and the subsequent spring, it would not be surprising to find summer-spawned bluefish 200 – 300 mm TL at the time of annulus formation. Studies utilizing length-based approaches to examine relative cohort contribution to the adult stock should further consider the influence of differences in cohort growth rates.

### *Conclusions and Future Work*

My results demonstrate that coastal ocean environments can function as important nurseries for juvenile bluefish, especially for summer-spawned individuals. Coastal habitats must possess the requisite resources and environmental conditions (e.g., abundant forage base and suitable temperatures) to fuel the high growth rates of YOY bluefish found in this study and reported elsewhere. Consequently, year class strength is influenced by factors governing growth and survival of juvenile bluefish in *both* estuarine and shallow coastal ocean habitats. Further, my hatch date analyses indicate that bluefish spawning is not strictly pulsed; therefore, the strict definitions of hatch dates of "spring" and "summer" cohorts and associated intra-annual pulsed recruitment pattern of juveniles to nursery habitats that have become prevalent in the bluefish literature, likely do not apply on a coast-wide scale and/or vary across years within and between nursery habitats.

Given the wide, and seasonally varying, latitudinal range of bluefish and their young along the eastern seaboard of the United States, important differences in recruitment dynamics likely exist among regions. Hence, a synoptic coast-wide study is needed to gain a comprehensive understanding of bluefish recruitment dynamics and controlling/regulating factors of recruitment. The current BlueCoast program is investigating coast-wide patterns (e.g., New York, New Jersey, Maryland (this study), and North Carolina) of bluefish recruitment dynamics within and between primary nursery habitats, the shallow coastal ocean and littoral estuarine habitats. Similarly, large-scale ichthyoplankton studies focused in the transitional (SAB → MAB) area of Cape Hatteras during late spring (May → June) might refine our understanding of bluefish reproductive biology. While ichthyoplankton studies have been conducted during June in the MAB (e.g., Smith et al. 1994; Norcross et al. 1974), concurrent collections from the SAB are lacking; these might prove useful in determining sources and transport dynamics of the recruits with early summer hatch dates observed in this study and by Takata (2004), but espoused by others to not exist, either because of low recruitment potential or lack of spawning.

A better understanding of movement patterns and residency of juveniles within and between nursery habitats would improve our knowledge of habitat utilization patterns. Traditional mark-recapture studies have been largely unsuccessful (Able et al. 2003); perhaps ultrasonic telemetry techniques might be applied to better understand movements/exchanges of juveniles within and among nursery habitats. Although telemetry techniques have been successfully applied for larger yearling bluefish (T. Grothues, personal communication), they may prove to be infeasible for small juveniles. Otolith microchemistry techniques showed initial promise (Takata 2004), and could be further developed and applied to better understand movements/residency of YOY bluefish.

# CHAPTER 2

## FORAGING ECOLOGY OF JUVENILE BLUEFISH IN MARYLAND COASTAL WATERS AND CHESAPEAKE BAY

Abstract: Coastal ocean environments may function as important feeding grounds for juvenile bluefish during the summer growing season. While food habits in estuarine environments have been extensively studied, little is known about the foraging ecology of juveniles in shallow coastal ocean habitats. I examined interannual, seasonal, and spatial (depth) patterns of diet composition of juvenile bluefish within and between coastal ocean (Maryland coastal waters) and estuarine (Chesapeake Bay) nursery habitats. Diet samples were analyzed from 2000-01/2003-04 and 1999-2004 collections in ocean and estuarine habitats, respectively. I also investigated availability trends (e.g., interannual and seasonal relative abundance) of principal prey. Further, predator-prey size relationships and size selectivity were evaluated for bluefish and bay anchovy in the coastal ocean. Juvenile bluefish were chiefly piscivorous across systems and habitats, with bay anchovy dominating diets in the coastal ocean and silversides dominating in littoral estuarine habitats. Diversity of piscine prey was higher in Chesapeake Bay than Maryland coastal waters. Juveniles in the coastal ocean appeared to switch to consumption of invertebrates (e.g., mysid shrimp) when bay anchovy abundances were relatively low (2003), suggesting a lack of alternative suitable piscine prey and increased reliance on invertebrates in coastal ocean v. estuarine habitats. Juvenile bluefish selected small, YOY bay anchovy (40 – 50 mm total length) in the coastal ocean. Highest abundances (500 – 1000 tow$^{-1}$) of YOY bay anchovy were observed in ocean habitats during late summer (August – October) when the summer cohort recruits to and is prevalent in coastal waters. The presence of an adequate bay anchovy forage base (by both abundance and size criteria) in coastal ocean habitats indicates that these environments can function as important nurseries for juvenile bluefish, especially summer-spawned individuals.

## Introduction

Predator-prey interactions and availability of prey (type, size, and abundance) play a pivotal role in mediating growth of young fishes, and therefore are important in shaping recruitment success. Predation in marine environments is highly size-structured; the lack of prey of appropriate sizes, those for which capture success may be low or handling times high, can result in decreased growth of predators, due to the relatively high energy costs incurred during foraging (Scharf et al. 1998; Juanes et al. 2001). Moreover, prey type and quality can affect growth rates. For instance, the availability and consumption of prey with higher energy densities (e.g., fish v. invertebrate prey) likely result in higher growth rates (Juanes and Conover 1994a), which may ultimately translate to higher recruitment success as faster-growing, larger individuals are better able to evade predators or may exhibit lower overwintering mortality (Sogard 1997) because they enter winter at a relatively large size.

The availability and encounter of piscine prey is especially important for sustaining juvenile bluefish. The onset of piscivory in young bluefish occurs fairly early in ontogeny, ~ 40 - 60 mm total length (Marks and Conover 1993), which coincides with the early juvenile period, when bluefish undergo a habitat shift, ingressing from offshore oceanic areas to near-shore nursery habitats (estuaries and the coastal ocean). Juanes et al. (1994) and Juanes and Conover (1995) hypothesized that accelerated onset of piscivory in young bluefish was facilitated by a temporal match between the movement of juvenile bluefish to estuarine nursery grounds (from spring-spawning in the SAB) with the peak production of small prey fishes (e.g., juveniles of silversides, *Menidia* sp.;

striped bass, *Moronoe saxatilis*; bay anchovy, *Anchoa mitchilli*). This idea is similar to Cushing's (1990) "Match-Mismatch" hypothesis extended to the juvenile stage.

Small bluefish are capable of nearly complete piscivory upon recruitment to nursery habitats, and remain chiefly piscivorous at larger sizes throughout the summer growing season. In the majority of diet studies, YOY bluefish in estuaries are mostly piscivorous (Grant 1962; Juanes et al. 1993; Juanes et al. 1994; Juanes and Conover 1995; Hartman and Brandt 1995a; Buckel and Conover 1997; Buckel et al. 1999b; Able et al. 2003; Scharf et al. 2004); yet some studies have documented the prevalence of invertebrate prey (e.g., shrimps and polychaetes) during particular years (Friedland et al. 1988) or at specific sites (Creaser and Perkins 1994; Harding and Mann 2001). Thus, juvenile bluefish appear to exhibit flexible foraging behaviors, consuming invertebrate as well as fish prey. YOY bluefish have very high consumption demands (20-30% body weight per day) and gastric evacuation rates (5.5 – 7 hours) in comparison to other temperate, estuarine associated fishes. For example, Hartman and Brandt (1995b) showed maximum daily consumption rates (at $20^{o}$ C) of YOY bluefish were at least 2-fold higher (0.16 $g\ g^{-1}d^{-1}$) than YOY weakfish (0.09 $g\ g^{-1}d^{-1}$) and YOY striped bass (0.040 $g\ g^{-1}d^{-1}$). Further, growth has been found to be significantly higher on a fish v. invertebrate-based diet (Juanes and Conover 1994a). Friedland et al. (1988) demonstrated that juveniles were in poorer condition (lower weight-at-length) in years when invertebrate prey dominated diets. Accordingly, juvenile bluefish would be expected to select habitats where they encounter abundant fish prey of appropriate sizes.

While the foraging ecology of juvenile bluefish has been well-studied in littoral estuarine habitats throughout the MAB (Grant 1962; Friedland et al. 1988; Juanes et al.

1993; Juanes et al. 1994; Creaser and Perkins 1994; Juanes and Conover 1995; Hartman and Brandt 1995a; Buckel and Conover 1997; Harding and Mann 2001; Able et al. 2003; Scharf et al. 2004); little is known about juvenile foraging ecology in coastal ocean environments. Able et al. (2003) and Buckel et al. (1999b) analyzed diet composition and prey selectivity (size and type) of juvenile bluefish collected from surf zone and deeper (> 20 m) continental shelf habitats, respectively. However, relatively few studies (Lassiter 1962; Lucena et al. 2000) have examined diet composition of bluefish in *shallow* (< 18 m) ocean habitats. Further, these studies either included age 1+ bluefish (> 300 mm) (Lucena et al. 2000) or it was not clear whether YOY were collected in surf zone or offshore (> 25 miles off Oregon Inlet) ocean habitats (Lassiter 1962). Interestingly, both Buckel et al. (1999b) and Lucena et al. (2000) found that engraulids dominated the diet of juveniles in coastal ocean, yet the former study was seasonally restricted to September and the latter occurred in Brazil. Here, I hypothesize that the strip of shoal coastal ocean habitat, < 18 m (and especially < 10 m), juxtaposed by deeper continental shelf waters and the surf zone, possesses an abundant supply of forage fish (primarily anchovies) throughout the summer growing season and thereby constitutes an important foraging area for YOY bluefish. To provide comparisons with estuarine YOY diet patterns, I investigated diet compositions of juveniles from open-water (mid-water trawl samples) habitats in both nearshore coastal waters and Chesapeake Bay. Further, diets of YOY from littoral habitats in both systems are described.

Coastal and estuarine habitats represent regions with differing seasonal availabilities of potential forage fish for juvenile bluefish. Comparison of recruitment strengths between habitats requires knowledge of diet composition because recruitment success depends upon encounter of YOY bluefish with small forage fishes. Furthermore, information regarding the foraging ecology of spring and summer cohorts within and between nursery habitats may provide insight into habitat suitability differences between cohorts and their relative contribution to the adult stock (see Chapter 1).

### *Objectives and Hypotheses*

My principal goal was to determine interannual, seasonal, cohort, ontogenetic, and spatial (depth) patterns of diet composition within and between coastal ocean (Maryland coastal waters) and estuarine (Chesapeake Bay) nursery habitats. Additionally, I evaluated predator-prey associations of YOY bluefish and their principal prey within and between habitats. Hypotheses were:

- Based on cohort representations (Chap. 1), YOY bluefish relative abundance is higher in coastal ocean habitats than Chesapeake Bay during late summer and fall
- Bay anchovy abundances are equivalent or higher in Maryland coastal waters v. Chesapeake Bay
- Abundances of bluefish and their primary prey are positively associated; both YOY bluefish and bay anchovy are most abundant at depths $< 10$ m
- Piscivory increases with size; nearly complete piscivory should occur beyond 80 mm total length. Prey size increases with bluefish size.
- In Chesapeake Bay, where both littoral and open water habitats were sampled, diets differ between these habitat types.

## Materials and Methods

### *Field Collections and Data Sources*

Samples and data from several survey programs were available: 1) Maryland coastal ocean, open-water, habitats; 2) Maryland surf zone habitats; 3) Chesapeake Bay open-water habitats; and 4) Chesapeake Bay littoral habitats. Open-water habitats in both systems were sampled using an 18-m$^2$ mouth-opening mid-water trawl, fished obliquely from surface to bottom in stepped intervals (one step every two minutes) for a total duration of 20 minutes. Field sampling of YOY bluefish in Maryland coastal open-water and Chesapeake Bay littoral habitats in 2003 and 2004 followed protocols described in Chapter 1. Coastal ocean sampling during 2000 (August, September) and 2001 (June, August, September) occurred in the same region as did 2003 and 2004 sampling; but rather than a stratified random design, transect sampling at fixed stations was employed. Three stations at depths of < 7, 7 – 12, and 13 – 20 m, respectively, were sampled along each of four north-south transects during a given cruise (Fig 2.1). I used data from August and September surveys in analysis of Maryland coastal open-water habitats (Table 2.1).

Mid-water trawl sampling in Chesapeake Bay was conducted as part of several bay-wide fishery independent surveys by the Chesapeake Biological Laboratory: TIES (Trophic Interactions in Estuarine Systems, 1995 – 2000, Edward Houde, P.I.), BITMAX (Biophysical Interactions in the Turbidity Maximum Zone, 2001 – 2003, Edward Houde, P.I.), and CHESFIMS (Chesapeake Bay Fishery Independent Multispecies Survey, 2001 – 2004, Thomas Miller, P.I.). TIES and CHESFIMS sampling occurred throughout the entire Chesapeake Bay, whereas BITMAX sampling was confined to the Upper Bay (38$^o$

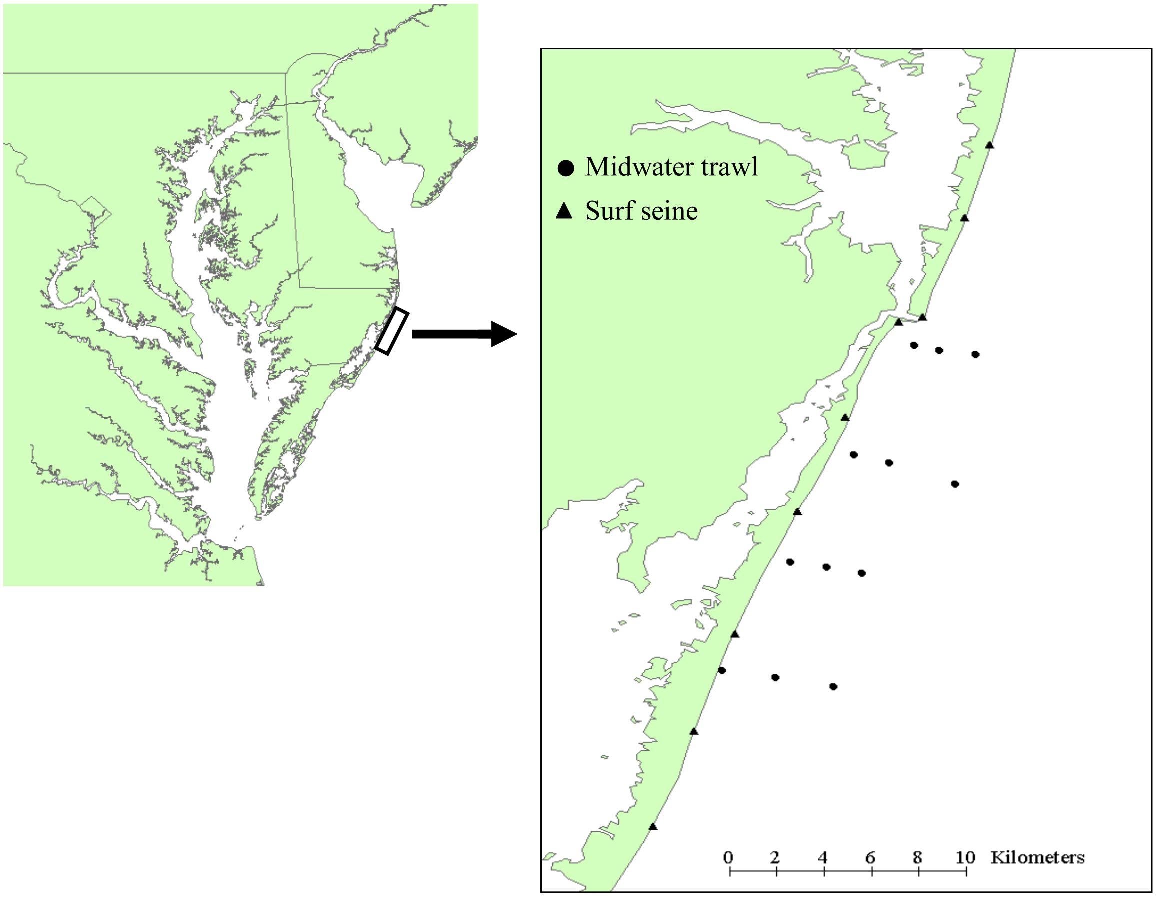


Figure 2.1. Fixed sampling sites for mid-water trawl collections in Maryland coastal waters during 2000 and 2001; surf zone seining in 2000, 2001, and 2004. Note the two northernmost and the extreme southern seine sites were not sampled in 2004, but were sampled in 2000 and 2001.

Table 2.1. Sample dates and deployments for mid-water trawl sampling in Chesapeake Bay and Maryland coastal waters, from which data was utilized in abundance (YOY bluefish and bay anchovy) and dietary (YOY bluefish) analyses. Survey definitions: TIES (Trophic Interactions in Estuarine Systems), BITMAX (Biophysical Interactions in the Turbidity Maximum Zone), CHESFIMS (Chesapeake Bay Fishery Independent Multispecies Survey), and BLUECOAST (trawl sampling in Maryland coastal waters). Note: Bottom trawl was employed for collections in the coastal ocean during 2004 (see Table 1.1, Chapter 1 for a summary of bottom trawl sampling efforts).

| System | Survey | Cruise Date | Season | No. Tows |
|---|---|---|---|---|
| | | 1999 | | |
| Ches Bay | TIES | July 7 – 17 | Early | 16 |
| Ches Bay | TIES | October 23 – 27 | Late | 28 |
| | | 2000 | | |
| Ches Bay | TIES | July 25 – 29 | Early | 40 |
| Ches Bay | TIES | October 17 – 21 | Late | 25 |
| Ocean | BLUECOAST | August 10 – 11 | Early | 12 |
| Ocean | BLUECOAST | September 20 – 21 | Late | 12 |
| | | 2001 | | |
| Ches Bay | BITMAX | July 6 – 14 | Early | 64 |
| Ches Bay | CHESFIMS | July 16 – 23 | Early | 48 |
| Ches Bay | CHESFIMS | September 25 – 29 | Late | 15 |
| Ches Bay | BITMAX | October 17 – 21 | Late | 44 |
| Ocean | BLUECOAST | August 15 – 16 | Early | 12 |
| Ocean | BLUECOAST | September 13 | Late | 12 |
| | | 2003 | | |
| Ches Bay | CHESFIMS | July 7 – 14 | Early | 51 |
| Ches Bay | BITMAX | July 28 – 30 | Early | 20 |
| Ches Bay | CHESFIMS | September 9 – 16 | Late | 29 |
| Ches Bay | BITMAX | October 21 – 23 | Late | 19 |
| Ocean | BLUECOAST | July 8 – 9 | Early | 16 |
| Ocean | BLUECOAST | July 29 – 30 | Early | 16 |
| Ocean | BLUECOAST | August 19 – 20 | Early | 16 |
| Ocean | BLUECOAST | September 24 – 25 | Late | 16 |
| Ocean | BLUECOAST | October 14 | Late | 16 |
| | | 2004 | | |
| Ches Bay | CHESFIMS | July 6 – 13 | Early | 51 |
| Ches Bay | CHESFIMS | September 13 – 21 | Late | 28 |

45’N – 39° 25’N, or from the upper Elk River downbay to the Chesapeake Bay Bridge) (Fig. 2.2). The number of sites sampled in TIES and CHESFIMS were typically allocated equally among major regions of Chesapeake Bay (e.g., upper, middle, and lower); sampling designs were either a combination of transect and randomized sampling (CHESFIMS) or solely transect sampling (TIES) (Jung and Houde 2003). Most sampling stations (70%) were in deeper channel regions of the mainstem (10 – 40 m depth); the remaining 30% were in more shoal regions (4 – 10 m depth). The complete range of depths sampled was 4 – 40 m. All mid-water trawl sampling in Chesapeake Bay was conducted at night (1900 – 0600), in contrast to coastal ocean collections, which were made during daylight (0700 – 1700). Three seasonal cruises (spring: April-May; summer: July; fall: September – October) were performed annually for each survey. I used diet and abundance data from July and September – October sampling (summer and fall) (Table 2.1). There was no sampling in the coastal ocean during 2002, and although sampling (mid-water trawl and seine) was conducted in Chesapeake Bay during 2002, diet samples were not available from this year and sampling effort in littoral habitats of Chesapeake Bay was low (n = 6 seine hauls). Therefore, data from 2002 was excluded from analyses.

YOY bluefish were collected with beach seines in littoral (< 2 m) habitats of Chesapeake Bay. All sampling occurred during daylight hours. Monthly collections were made by the Maryland Department of Natural Resources (DNR) from July – October during 1999 – 2001 at fixed stations (~30) throughout Maryland’s portion of Chesapeake Bay (same stations as those presented in Fig. 1.1, Chapter 1, for 2004 sampling). A 30.5 m x 1.24 m bagless, untreated beach seine was used in this survey.

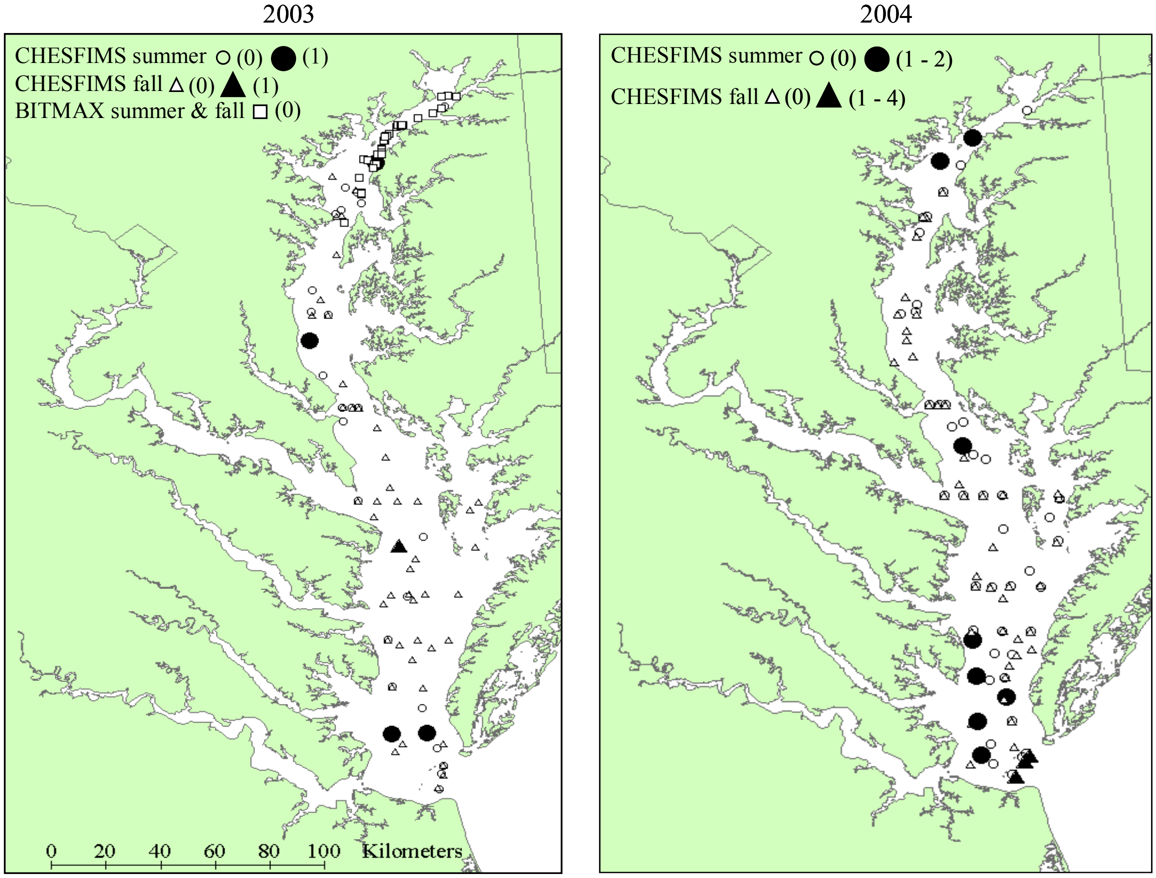


Figure 2.2 Sample sites for mid-water trawl deployments in Chesapeake Bay during 2003 and 2004. Filled symbols denote presence of YOY bluefish; catch ranges (given parenthetically) of YOY bluefish at particular stations reported. Summer = July for both BITMAX and CHESFIMS surveys; Fall = October for BITMAX and September for CHESFIMS.

Our laboratory group conducted weekly seine collections at the Chesapeake Biological Laboratory research pier from June to September during 1999 – 2001, 2003, and 2004 (Table 2.2), using a 1.5 m x 30.5 m beach seine (with a bag and untreated netting). The substrate at this site is composed mostly of mud, with some sand, and no vegetation or habitat relief except the riprap along the shore, which is submerged during flood tide. Three seine hauls were conducted the same day each week on either side of the pier (one hour before low tide). The seine was hauled parallel to shore for two hauls on the eastern side of the pier, whereas the seine was fully extended perpendicular to shore and hauled to shore in a quarter-circle sweep for the single (catch-per-unit effort, CPUE) haul on the western side of the pier. Catch data (YOY bluefish, anchovies, and silversides) from the standardized CPUE seine haul were utilized to examine seasonal and interannual abundance patterns of YOY bluefish and their primary prey. YOY bluefish from all hauls were retained for diet analysis.

Seining also was conducted in exposed, surf zone habitats along Maryland's coast. Nine fixed beach sites on the barrier islands of Fenwick (n = 3) and Assateague (n = 6) (Fig. 2.1) were sampled monthly from June to September during 1999 – 2001, and 2004 (Table 2.2). The southernmost and northernmost sites on Fenwick and Assateague Island were located adjacent to rock jetties that bordered the Ocean City Inlet. A large and durable beach seine was required for seining in Maryland's energetic surf zone environment, in which wave heights are typically 0.5-1 m. We deployed a 30.5 x 1.8 m tarred beach seine with a bag. The seine was extended parallel to shore once a depth of ~1.5 m was reached, and hauled to shore with the assistance of two persons on the beach pulling ropes attached to steel brails. We used the criterion that one "successful" haul be

Table 2.2. Sample dates for seine collections in littoral habitats of estuarine (Chesapeake Bay) and oceanic (surf zone) habitats. Sampling in Chesapeake Bay, at the Chesapeake Biological Laboratory research pier, was generally weekly. In surf zone habitats, nine fixed stations were sampled each month.

| Chesapeake Bay | Surf Zone |
|---|---|
| 1999 | |
| June 9, 22, 24 | N/A |
| July 29 | |
| September 17 | |
| 2000 | |
| May 31 | June 20 – 21 |
| June 8, 14, 19, 28 | July 15, 18, 20 |
| July 7, 13, 18, 25, 31 | August 16 |
| August 8, 9, 18, 24, 31 | September 16, 17 |
| September 14, 29 | |
| 2001 | |
| May 17, 23, 31 | June 11, 12 |
| June 7, 13, 18, 25 | July 16, 17 |
| July 5, 11, 27 | August 13 |
| August 2, 9, 22, 30 | September 10, 11 |
| September 5, 14, 21 | |
| 2003 | |
| June 3, 10, 17, 27 | N/A |
| July 1, 11, 15, 25, 31 | |
| August 6, 14, 21, 29 | |
| September 5, 11, 20 | |
| October 8 | |
| 2004 | |
| May 13, 21, 27 | July 29 |
| June 3, 10, 17, 24 | Aug 25 |
| July 1, 15, 22, 30 | September 21, 24 |
| August 6, 12, 19, 30 | |
| September 2, 9, 15 | |
| October 1, 8, 15 | |

completed per station because more than one haul per station was sometimes required due to rolling of the bag or participants becoming detached from brails due to wave action. YOY bluefish catches were low and sporadic in surf zone environments; hence, I only present a qualitative description of diet composition. In total, diets of only 19 individuals from the surf zone were analyzed.

All YOY bluefish collected across various habitats and gears were enumerated and measured (total length, TL) to the nearest millimeter. YOY bluefish were either placed on ice or preserved in 95% ethanol for later diet analysis. Anchovies (*Anchoa mitchilli* and *Anchoa hepsetus*) were also enumerated and measured (30 individuals); abundances were typically estimated by gravimetric subsampling due to large catches (especially in mid-water trawl collections).

### *Diet Analysis*

A total of 1,641 stomachs of juvenile bluefish, 35 – 290 mm TL, were analyzed. Diets of all collected juveniles were analyzed, except those from 2004 bottom trawl collections in the coastal ocean, from which subsamples (total n = 451) were taken (see Chapter 1). Prey items were identified to the lowest possible taxonomic level, typically family or genus. Piscine prey was often highly masticated and otherwise difficult to identify, likely attributed to high digestion rates. Accordingly, hard part keys (vertebrae, scales, and otoliths) were constructed for c. 15 families and 30 species of fish prey common in bluefish guts in our preliminary diet analyses and/or reported in other studies. Diagnostic morphological characteristics of hard parts, particularly vertebrae, enhanced identification of piscine prey to the family level (Lassiter 1962; Hansel et al. 1988; Scharf et al. 1997; Scharf et al. 1998). For instance, vertebral parapophyses and centra of silversides are very robust in comparison to anchovies; clupeids have thin, elongate hemal and neural spines, in addition to a higher number of intermuscular bones (e.g., epipleurals) relative to other piscine prey items (Fig. 2.3). Stomachs that were either completely empty or held only refractory material (e.g., fish scales, sand grains, rocks, grass blades, macroalgae, monofilament fishing line) were classified as empty. If only scales, fin rays, opercles, branchiostegal rays, etc. of pisince prey were present, with no attached flesh, the stomach was designated as empty, although the presence of these piscine remains was used to increase the sample size for an index of piscivory for 2003 and 2004 samples (see Statistical Analyses). The same classification of empty stomachs was employed for 1999 – 2001 samples, but the presence of piscine remains in "empty" stomachs was not recorded for those samples.

Incidence and weights of prey items were recorded. All individuals of a given prey type were blotted dry, and their composite wet weight measured, to the nearest milligram, using a Mettler-Toledo microbalance. Additionally, weights of juvenile bluefish (before gut extraction) and whole stomachs (both full and purged of gut contents) were taken. Only incidence metrics (e.g., percent frequency of occurrence (%FO), Hyslop 1980) were included in statistical analyses of diet composition, because I had little confidence in estimates of dietary importance (i.e., relative percent weight of prey items, %W). For instance, due to the high partial digestion rates and our inability to back-calculate weight at consumption, highly digested fish prey (e.g., present only as an axial skeleton with little attached flesh) might result in a similar importance value by weight as a few sand shrimp that are not as rapidly digested; consequently, the

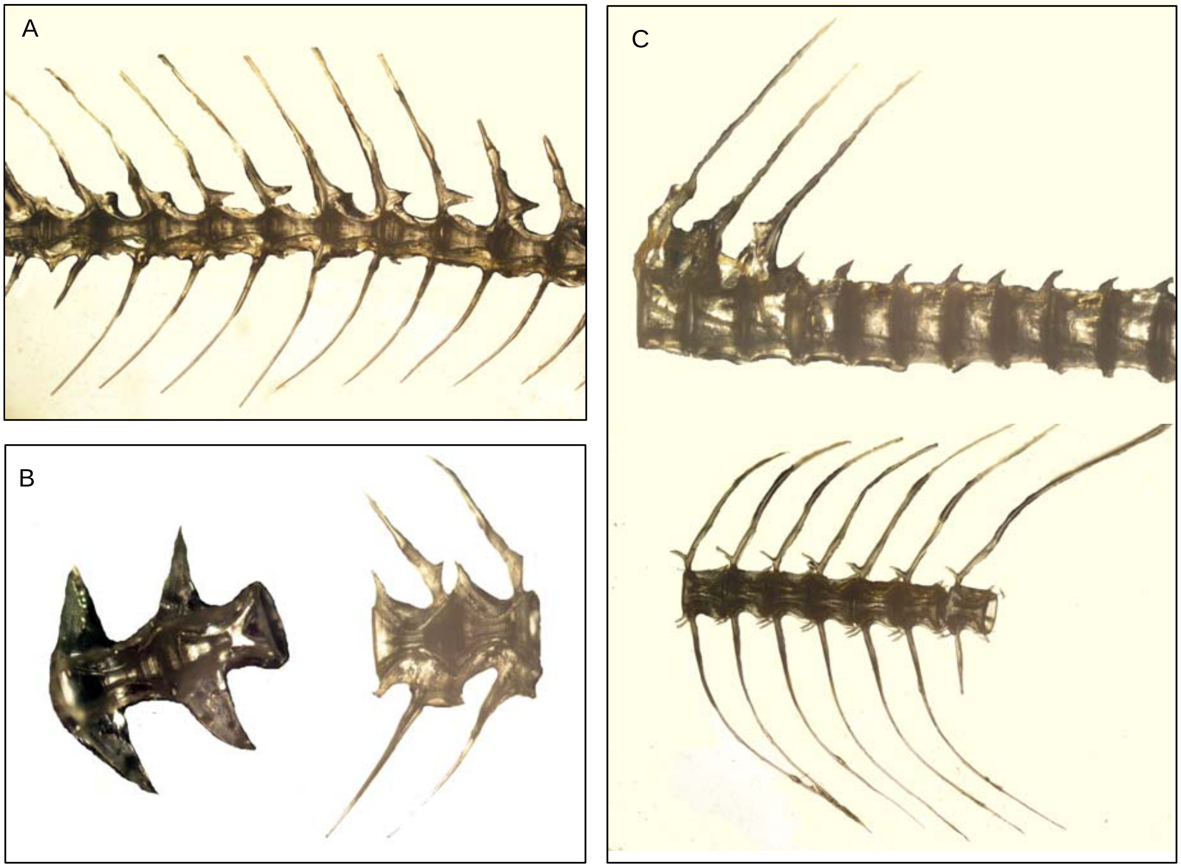


Figure 2.3. Representative vertebrae samples used to identify piscine prey to family level. A: Bay anchovy vertebral column – mid-body; B: Atlantic silverside vertebrae – anterior (left) and mid-body (right); C: Atlantic menhaden vertebrae - anterior portion (top) and hickory shad vertebrae - mid-body (bottom).

importance of the piscine prey would likely be underestimated. Alternatively, % FO (here the percent of bluefish with one or more items of a particular prey type in their gut relative to the total number of bluefish with food in their guts), is less influenced by high digestion rates than %W. Therefore, relative percent weight (%W), expressed as the contribution of a prey item to the total weight of all prey in the stomach, averaged across all individuals examined (Hyslop 1980), was calculated and used in a descriptive manner.

For years 2003 and 2004 (ocean samples), I conducted a study of relative prey size. Total lengths of piscine prey were measured to the nearest millimeter. However, most piscine prey were present in pieces rather than whole form. Therefore, I measured caudal peduncle height (CP) and/or eye diameter (ED, for head pieces with intact eyes, i.e., not just orbital height) of bay anchovy prey to reconstruct original prey lengths using regressions developed by Scharf et al. (1997):

$$TL = 16.009*ED + 1.257 \qquad r^2 = 0.97 \qquad (1)$$

$$TL = 11.312*CP + 2.662 \qquad r^2 = 0.96 \qquad (2)$$

When both CP and ED measurements were possible for the same bay anchovy, the average TL obtained from equations 1 and 2 was used as the original prey length. Also, total length measurements of whole bay anchovy prey attributed to net feeding (see below) were not included in analyses of predator-prey length relationships. Recovered striped anchovy prey were also measured, yet due to low sample sizes (n =14 bluefish, across years, with striped anchovy in their guts) predator size-prey size relationships were not analyzed for striped anchovy. Measurements of prey were made using an ocular micrometer, and recorded to the nearest tenth of a millimeter. Analyses were restricted to ocean samples in 2003 and 2004, because these were carefully preserved on dry ice to retard degradation of diet items. Low sample sizes from Chesapeake Bay in 2003 and 2004 precluded a similar analysis for that system. For instance, regression equations for CP and ED have been developed for Atlantic silverside prey in addition to anchovies (Scharf et al. 1997), yet only 5 silverside and 4 bay anchovy prey specimens were suitable for measurement across years for Chesapeake Bay collections.

During a twenty minute trawl tow, some captured bluefish feed within the net (Buckel et al. 1999). This artificial feeding behavior, net feeding, can bias diet indices of percent occurrence, weight, and gut fullness. I attributed piscine prey (mainly anchovies) which showed little signs of digestion and appeared in a fresh state to net feeding. This designation was subjective; generally, if the whole prey body was recovered, or severed into two fresh pieces, with scales/flesh intact, net feeding was assumed. Additionally, the presence of anchovy prey within the mouth or esophagus of captured bluefish was also considered net feeding. Potential net feeding was evaluated only for juveniles collected with trawls, across systems, during 2003 and 2004. If all contents of a given prey type were judged to be derived exclusively from net feeding, the prey category was not scored positive for incidence, nor was its weight measured. Otherwise, if the same prey item was present in two states, fresh (i.e., net feeding) and digested, incidence was unaffected (i.e. positive), and weight measurements only included prey not associated with net feeding.

### Statistical Analyses

#### *Diet*

I employed chi-square tests of independence to test for differences in incidence of respective prey items (1-way cross tabulation) among levels of the class variables: year, season, and depth (Table 2.3). Fisher's Exact test was employed to evaluate hypotheses if expected cell counts were less than five. Diet comparisons were restricted to similar gear types, and typically made within a particular system and habitat (Table 2.3). Diet composition was compared between years within a given system. For 2003 and 2004 samples (both ocean and Chesapeake Bay), efforts were made to identify anchovies to the species level (*A. mitchilli* v. *A. hepsetus*); however for 1999 – 2001 samples, anchovies were not identified to the species level. Hence, for statistical comparisons, a general 'anchovy' category was used (ignoring species identification). Information on the proportions of bay:striped anchovy for specimens that could be positively identified was used in a descriptive context. I evaluated seasonal differences in diet within each year in a given system and habitat. Seasons were designated 'early' and 'late' for periods July – August 31 and September 1 – November 4 for coastal ocean samples, respectively, and May – July 31 and August 1 – October for Chesapeake Bay samples. The slightly different seasonal designations between systems were adopted because of the general earlier occurrence of YOY bluefish in Chesapeake Bay v. coastal ocean environments (see Chapter 1). I contrasted diets of juvenile bluefish collected in shoal ($\leq$ 10 m) and deep (> 10 m) regions in Chesapeake Bay and Maryland coastal waters, pooling data across years. The only direct comparison of diet composition between Chesapeake Bay and Maryland coastal waters was that for 2001 mid-water trawl data, because this was the

Table 2.3. Summary of diet comparisons and associated data sources and gear types.

| System | Gear | Data: Years (Months) | Comparisons |
|---|---|---|---|
| Coastal Ocean | Mid-water trawl | 2000-01 (Aug, Sep)<br>2003 (Jul, Aug, Sep, Oct) | Year (200-01, 2003)<br>Season (2003 only)<br>Depth (pooled across years)<br>System (2001 only) |
| | Bottom trawl | 2004 (Jul, Aug, Sep, Nov) | Depth<br>Season |
| | Surf seine | 1999-01, 2004 (Jun-Sep) | Pooled, descriptive analysis |
| Chesapeake Bay | Mid-water trawl | 1999 (Jul, Oct)<br>2001 (Jul)<br>2004 (Jul, Sep) | Year (1999, 2001, 2004)<br>Season (1999 only)<br>Depth (pooled across years) |
| | Beach seine | 1999-2001 (Jun-Sep)<br>2003-2004 (Jun-Sep) | Year (1999-2001, 2003-04)<br>Season (by year) |

only year when comparable diet data (i.e., same gear type and concurrent collection seasons) was available. Mid-water trawl sampling was also conducted in both systems in 2003; however, only one bluefish from Chesapeake Bay sampling was available for that year. Finally, for ocean samples in 2003 and 2004, diets were compared between spring and summer cohorts (only those individuals directly aged and assigned to a particular cohort). In these cohort analyses, each fish was considered an independent observation.

Incidence was estimated as the percent of hauls or tows for which one or more bluefish consumed a particular prey type. For chi-square tests of prey incidence, I defined all bluefish collected in a given haul/tow on a particular sampling date as an independent observation, rather than treating each individual fish as an independent observation. For example, incidence of mysids would be scored positive whether one or all juvenile bluefish from a given tow had consumed them. Only hauls/tows where one or more bluefish contained prey (i.e., not empty) were used in incidence calculations. Defining the sampling unit as all fish from each tow/haul considerably reduced the degrees of freedom in chi-square analyses. However, the rationale for treating the data this way is that juvenile bluefish travel and feed in schools (Juanes and Conover 1994b). Thus, the diet composition of individuals collected in the same haul/tow on a particular date would be expected to be similar (i.e., autocorrelated and not independent). Moreover, if each fish is treated as an independent observation, then associated diet indices may be skewed or biased towards hauls/tows where high catches were observed. Buckel et al (1999a) and Buckel et al. (1999b) used an approach similar to mine, whereby all captured bluefish from a given tow/haul were designated as a sampling unit; yet their calculations of mean %FO were more complex as they used cluster sampling estimators.

Principal components analysis (PCA) was used to explore patterns of prey item co-occurrence. Data for this analysis was pooled across years for similar gear types within each system and habitat (e.g., Chesapeake Bay seine data). The sampling unit was each tow or haul. Component loadings of the first three factors (standardized eigenvalues) were plotted. Factor scores were analyzed for effects of year, season and depth using Kruskal-Wallis tests because factors scores were not normally distributed.

To evaluate my hypothesis that juvenile bluefish were nearly completely piscivorous by 80 mm TL, I used chi-square tests of independence to compare incidence of piscine prey between bluefish of sizes ≤ 80 mm TL and > 80 mm TL. Additionally, I employed the same test to determine if percent piscivory differed among five size classes: ≤ 80, 81 – 120, 121 – 160, 161 – 180, 181 – 200, and > 200 mm TL. Data for these analyses were pooled across years for similar gear types within each system and habitat (e.g., coastal ocean, mid-water trawl). For this analysis, each individual fish represented an independent observation. The presence of all piscine remains was used to estimate an index of piscivory for 2003 and 2004 samples. However, because data were pooled over years for a particular gear type, and this classification scheme was not used for 1999 – 2001 data, the index of piscivory for analyses was based only on bluefish with food in their stomachs.

Least-squares linear regression was used to test predator size-prey (bay anchovy) size relationships. I used Analysis of Variance (one-way ANOVA) to test for shifts in foraging modes of juvenile bluefish, namely to discern whether predator-prey total length ratios were smaller for bay anchovy consumed whole v. partially (*sensu* Scharf et al. 1997). Also, I examined prey size selectivity by comparing bay anchovy lengths recovered in bluefish guts to lengths collected in trawls for given cruises in the coastal ocean where there was sufficient data (October 2003; July 2004; August 2004; September 2004). Because length distributions of prey were typically non-normally distributed, median tests (Zar 1996) were employed to test for differences in medians of gut and field length frequency distributions of bay anchovy (Juanes et al. 1994; Juanes and Conover 1995; Scharf et al. 1997).

### *Abundance/Occurrence*

I examined occurrence and abundance patterns of YOY bluefish and their principal prey within and between systems and habitats. Like diet comparisons, abundance comparisons were restricted to similar gear types. Bluefish catch data from mid-water trawl sampling in Maryland coastal waters and Chesapeake Bay contained many zero catches, and data did not meet parametric assumptions of normality of residuals or homogeneity of variance among groups of class variables, despite data transformations (e.g., ln (n + 1)). Consequently, I statistically tested bluefish occurrence rather than relative abundance (e.g., mean CPUE or catch-per-tow). I used available catch data from July to October in each system (Table 2.1) to calculate mean annual occurrence. Then, I employed the logit model, a generalized linear model form of logistic regression, to test for system and year (within system) differences in bluefish occurrence. Because exclusively discrete class variables (e.g., year and system) were used in logistic regression analyses, traditional goodness-of-fit-measures (e.g., Homer-Lemeshow, likelihood ratios) could not be calculated because they require at least one continuous variable (Kutner et al. 2003). Therefore, I calculated McFadden $r^2$ values to assess goodness-of-fit of the model. This $r^2$ value is valid when discrete predictor variables are used, and its interpretation is analogous to an ordinary $r^2$ (e.g., the coefficient of determination in least-squares linear regression) (McFadden 1974). Where McFadden $r^2$ values indicated a poor model fit, separate pairwise chi-square tests of independence were performed. For comparisons of bluefish occurrence between systems (Chesapeake Bay v. Maryland coastal waters), I used data from years when concurrent sampling was conducted in each system (2000, 2001, and 2003) and employed a two-way logit model including both year and system (with an interaction term). Additionally, I pooled data within each system across years and used a chi-square test of independence to test for system effects. Finally, one-way logistic regression models were used to test for year effects within each system. Multiple mean comparisons (employing Bonferroni-adjusted experiment-wise error rates) were performed to determine in which years mean incidence was significantly different than others.

Bay anchovy catch data from mid-water trawl sampling in both systems exhibited extreme variation, with catch-per-tow varying by four orders of magnitude (e.g., 0 – 35,000 per tow for Chesapeake Bay; 0 – 15,000 per tow for Maryland coastal waters). Catch data, raw or transformed, did not meet assumptions of parametric analyses. Therefore, non-parametric techniques were utilized to evaluate bay anchovy abundance patterns, in which abundances were converted to ranks. I used the Scheirer-Ray-Hare extension of the Kruskal-Wallis test (Sokal and Rohlf 1995) to compare bay anchovy abundance between systems, again using data from concurrent years of sampling within each system, 2000, 2001, and 2003. This test is a nonparametric two-way ANOVA (with ranks as the dependent variable), and the associated test statistic is the H-statistic, which is distributed as a $\chi^2$ variable (Sokal and Rohlf 1995). I used a traditional one-way

Kruskal-Wallis test to test for global interannual differences in bay anchovy abundance within each system and nonparametric Tukey-type multiple comparisons (Zar 1996) to evaluate specific interannual differences in bay anchovy abundance. I also compared the abundance of striped anchovy between systems, based on mid-water trawl data from 2000, 2001, and 2003 using the same nonparametric two-way ANOVA described above.

YOY bluefish occurrence/abundance and bay and striped anchovy abundance were compared between depth zones ($\leq$ 10 m and > 10 m) within each system (trawl data only). I used chi-square tests of independence to evaluate differences in bluefish occurrence between depth zones using mid-water trawl data pooled across years within each system. I used the non-parametric Wilcoxon two sample t-test to test for differences in bay and striped (coastal ocean only) anchovy abundance between depth regions. The effect of depth on 2004 ocean bottom trawl estimates of YOY bluefish (see Chapter 1 for methods on standardized abundance estimates) and bay and striped anchovy abundance was tested with a Wilcoxon two sample t-test. For bay and striped anchovy abundance, separate analyses were performed for the two tow durations (10 and 20 minute tows) because it was impossible to standardize anchovy abundances due to the large variations in catches.

For littoral habitats, only data from seine catches in Chesapeake Bay at the Chesapeake Biological Laboratory were used to test for seasonal and interannual abundance/occurrence trends of YOY bluefish , *Anchoa* sp., and *Menidia* sp. (Table 2.2). Seine sampling is rather qualitative (Able 1999). Thus, I focused only on analysis of occurrence metrics for YOY bluefish and primary forage fishes. Standard errors of seine catches were typically greater in amplitude than mean annual or seasonal catch-per-unit effort metrics for forage fishes and YOY bluefish. This is likely attributed to 'hitting' or 'missing' large patches of these schooling fishes during seining. All *Menidia* sp. and *Anchoa* sp. were pooled into general categories of 'anchovy' and 'silversides'. I used chi-square tests of independence to test for differences in occurrence of each species between seasons (years pooled and by year) and among years. Data from 1999 were not used in year-specific seasonal comparisons due to inadequate sampling in that year (Table 2.2).

## Results

### Diet Composition and Comparisons

#### Coastal Ocean

Fish prey dominated the diets of YOY bluefish collected by trawls in Maryland coastal waters, typically comprising 80-95% of the diet by both incidence and weight across years (Table 2.4). Anchovies were principal prey. Based on stomachs containing anchovy prey that could be identified to species level, bay anchovy were more common than striped anchovy. Of 25 stomachs in 2003: 15 (60%) contained bay anchovy, 9 (26%) striped anchovy, and 1 (4%) both bay and striped anchovy. Of 46 stomachs in 2004: 40 (87%) contained bay anchovy, 4 (9%) striped anchovy, and 3 (7%) both bay and striped anchovy. Less common (< 4 percent frequency of occurrence, %FO) fish prey were clupeids, butterfish (*Peprilus triacanthus*), sciaenids, and silversides (*Menidia* sp.) (Table 2.4). Cannibalism was rare (1.4% FO) and only observed in 2004. Rare fish prey included northern sennet (*Sphyraena borealis*), mullets (*Mugil sp.),* and larvae of several

Table 2.4. Diet composition of juvenile bluefish collected in Maryland coastal waters during 2000, 2001, 2003, and 2004. Mid-water trawl was employed for collections in 2000, 2001, and 2003; bottom trawl was used in 2004. Percent frequency of occurrence (%FO) and relative percent weight (%W) indices were calculated on a per fish basis (only individuals with food in their guts). The number of bluefish guts containing a particular prey item is given parenthetically. For 2000 and 2001 data, anchovy prey was not identified to species level and miscellaneous prey categories were not recorded. Diet indices for *Anchoa* sp. prey category were calculated from pooled anchovy prey items: *A. mitchilli, A. hepsetus*, and unidentified anchovy prey. Macroalgae was generally *Aghardelia* sp.; seagrass was *Zostera marina*. Debris category encompasses sand grains, rock, petrified wood material, plastic, wire, and monofilament fishing line. %W was not calculated for miscellaneous categories.

| Prey type | 2000 | | 2001 | | 2003 | | 2004 | |
|---|---|---|---|---|---|---|---|---|
| | %FO | %W | % FO | %W | % FO | %W | % FO | %W |
| FISH | 94.6 (27) | 94.5 | 82.6 (123) | 81.3 | 74.2 (115) | 68.4 | 94.1 (270) | 92.4 |
| *Anchoa* sp. | 78.6 (22) | 76.3 | 66.4 (99) | 63.1 | 44.5 (69) | 42.2 | 85.0 (244) | 83.3 |
| *Anchoa mitchilli* | | | | | 64 (16) | 54.0 | 93.5 (43) | 87.1 |
| *Anchoa hepsetus* | | | | | 40 (10) | 40.2 | 15.2 (7) | 11.5 |
| Clupeidae | 3.6 (1) | 3.6 | 3.4 (5) | 2.6 | 2.6 (4) | 2.4 | | |
| *Menidia* sp. | | | 0.7 (1) | 0.7 | 3.9 (6) | 3.8 | 1.0 (3) | 0.8 |
| Sciaenidae | | | 0.7 (1) | 0.3 | 0.6 (1) | 0.7 | 1.4 (4) | 1.1 |
| *Peprilus triacanthus* | | | | | 0.6 (1) | 0.1 | 3.5 (10) | 2.1 |
| *Mugil* sp. | 3.6 (1) | 3.6 | 0.7 (1) | 0.1 | | | | |
| *Pomatomus saltatrix* | | | | | | | 1.4 (4) | 0.7 |
| *Sphyraena borealis* | | | | | 0.6 (1) | 0.5 | | |
| UnID fish | 42.9 (12) | 11.2 | 15.4 (23) | 14.6 | 11.6 (18) | 9.3 | 6.3 (18) | 4.5 |
| ICHTHYOPLANKTON | | | | | | | | |
| Fish larvae | | | | | 17.4 (27) | 9.0 | | |
| *Micropogonias undulatus* | | | | | 5.8 (9) | 2.7 | | |
| Clupeidae[a] | | | | | 2.6 (4) | 1.6 | | |
| *Anchoa* sp. | | | | | 1.9 (3) | 0.7 | | |

Table 2.4 con't…

| Prey type | 2000 | | 2001 | | 2003 | | 2004 | |
|---|---|---|---|---|---|---|---|---|
| | %FO | %W | % FO | %W | % FO | %W | % FO | %W |
| *Stenotomus chrysops* | | | | | 0.6 (1) | 0.7 | | |
| UnID fish larvae | | | | | 6.5 (10) | 3.5 | | |
| Fish eggs | | | | | 2.6 (4) | 0.7 | 0.3 (1) | 0.1 |
| UnID fish eggs | | | | | 1.3 (2) | 0.7 | 0.3 (1) | 0.1 |
| INVERTEBRATES | 10.7 (3) | 5.5 | 28.9 (43) | 18.7 | 53.5 (83) | 31.6 | 10.5 (29) | 7.6 |
| Mysid shrimp | 7.1 (2) | 1.8 | 17.5 (26) | 10.2 | 34.2 (53) | 16.8 | 6.3 (18) | 4.5 |
| *Crangon septimspinosa* | | | | | 7.7 (12) | 4.0 | | |
| Shrimp zoea | | | | | 0.6 (1) | 0.2 | | |
| *Alpheus* sp. | | | | | | | 0.3 (1) | 0.4 |
| Crab megalopae | | | 0.7 (1) | 0.4 | 9.0 (14) | 3.1 | 0.7 (2) | 0.5 |
| Crab zoea | | | | | | | 0.3 (1) | |
| Hermit crab | | | 1.3 (2) | 0.8 | | | | |
| Calanoid copepod | | | | | 9.0 (14) | 2.4 | | |
| Caligidae copepod | | | | | 1.3 (2) | 0.7 | | |
| Polychaete (*Nereis sp.*) | | | 0.7 (1) | 0.7 | 1.3 (2) | 0.7 | | |
| Squid | | | 0.7 (1) | 0.7 | 0.6 (1) | 0.6 | 0.3 (1) | 0.1 |
| *Tagelus* sp. | | | | | | | 0.7 (2) | 0.4 |
| *Lampsilis* sp. | | | | | 0.6 (1) | 0.02 | | |
| Gammarid amphipod | | | 0.7 (1) | 0.02 | 0.6 (1) | 0.6 | | |
| Corophiid amphipod | | | | | 0.6 (1) | 0.2 | | |
| Chaetognath | | | | | 0.6 (1) | 0.02 | | |
| UnID crustacean | 3.6 (1) | 3.6 | 8.7 (13) | 5.9 | 7.1 (11) | 2.1 | 2.0 (6) | 1.8 |
| MISCELLANEOUS | | | | | | | | |
| Macroalgae | | | | | 5.8 (9) | | | |
| Seagrass | | | | | 3.2 (5) | | 2.1 (6) | |
| Debris | | | | | 5.8 (9) | | 2.1 (6) | |

Table 2.4 con't…

| | 2000 | 2001 | 2003 | 2004 |
|---|---|---|---|---|
| No. bluefish examined | 30 | 219 | 211 | 451 |
| % (No.) empty stomachs | 6.7 (2) | 32 (70) | 26.5 (56) | 36.4 (164) |
| Total length range (mm) | 88 – 258 | 80 – 242 | 75 – 290 | 68 - 200 |

[a] Includes *Clupea harengus, Opisthonema oglinium*, and unID clupeid larvae

taxa. Unidentified fish prey typically comprised < 15% and < 10% of the diet by occurrence and weight, respectively, across years.

Invertebrate prey were especially common in 2003 (54% FO, 32% W), but only moderately common in other years (11 – 29% FO) when they contributed minimally to diet biomass (6 – 19 %W). Mysid shrimp was the dominant invertebrate prey. All mysid prey, for samples in both Maryland coastal waters and Chesapeake Bay in 2003 and 2004, were identified as *Neomysis americana*; except for one bluefish sample from the coastal ocean which contained an unidentified larger mysid. Mysids were not identified to species level for 1999 – 2001 samples, but it is likely the majority were *N. americana*. Other invertebrate prey were diverse, yet rare (<1% FO) across years, with the exception of 2003, when crab megalopae, sand shrimp (*Crangon septimspinosa*), and calanoid copepods were observed in 9% of samples. Unidentified crustaceans were < 9% and <6% of the diet by occurrence and weight, respectively, across years. Fish larvae (Atlantic croaker, clupeids, and anchovy) were only present in stomachs from 2003 collections. The percent frequency of occurrence of fish larvae was 17.4%. The occurrence of empty stomachs was c. 30% across years, except for 2000 (7%).

The diet composition of YOY bluefish collected by mid-water trawl in the coastal ocean differed significantly among years (Fig. 2.4). Diets in 2000 and 2001 were similar: anchovy occurred at 100% incidence, and mysids were relatively common (30 – 50% incidence). Recall here that incidence values were calculated as the percent of *tows* from which one or more bluefish consumed a particular prey - see Methods. Diets in 2003 were more diverse, with a decreased contribution of fish prey and increased contribution of invertebrate prey relative to 2000 and 2001. The incidences of fish and anchovy prey

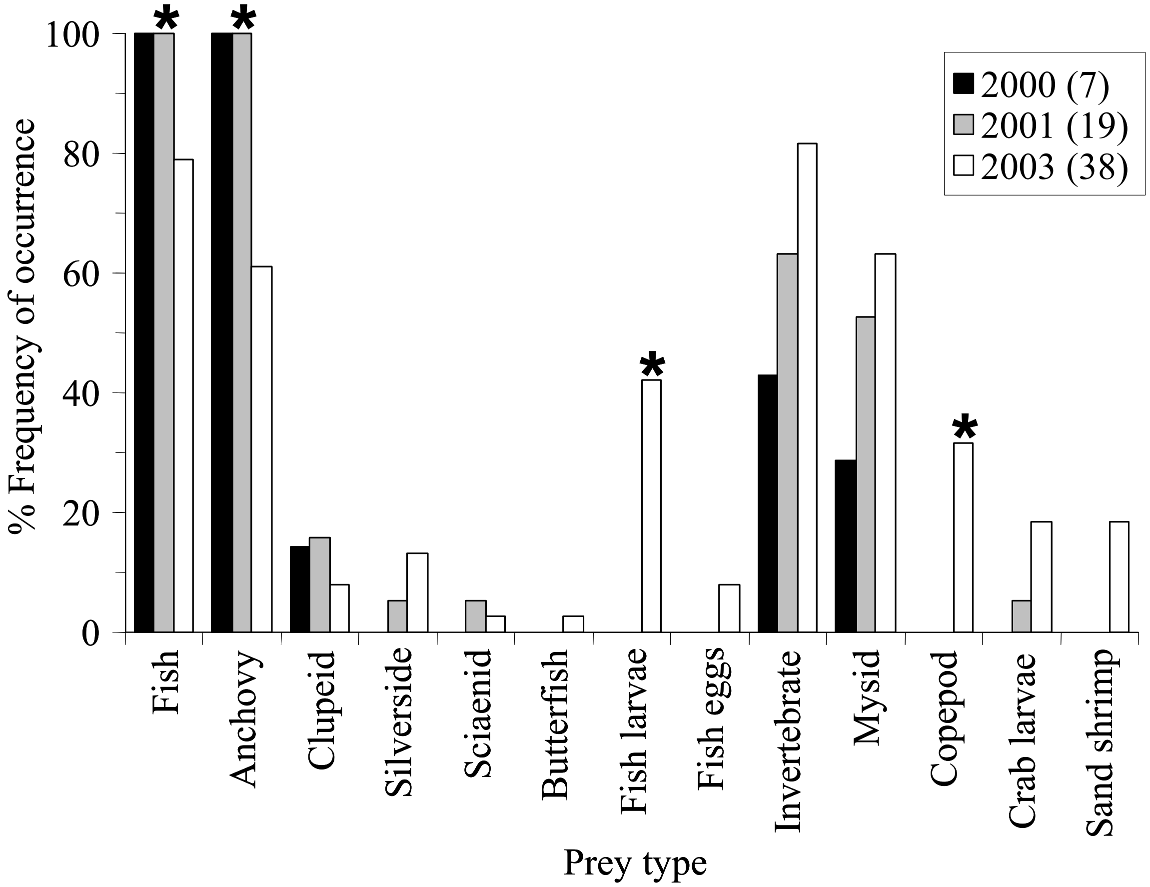


Figure 2.4. Annual diet composition of juvenile bluefish collected in Maryland coastal waters with mid-water trawl. %FO reported as the percent of tows from which one or more bluefish guts contained a particular prey type. Total number of tows with bluefish each year is given parenthetically. Asterisks denote significant differences in %FO among years for a given prey item, based on chi-square tests of independence.

were significantly lower in 2003 v. 2000 and 2001 ($p < 0.0001$ fish; $p = 0.03$ anchovy). Fish larvae and calanoid copepods were only present in 2003 and exhibited a significantly higher incidence in 2003 v. 2000 and 2001 ($p < 0.0001$ fish larvae, $p = 0.005$ calanoid copepods). Sand shrimp, butterfish, and fish eggs were only observed in 2003. Diet data from 2004 were not included because the mid-water trawl was not used in that year. However, diets in 2004 were similar to those in 2000 and 2001 (Table 2.4), with anchovy as the dominant prey item and mysids and unidentified fish ranking next in occurrence.

No significant seasonal differences in diet were observed for 2003 or 2004 collections. Invertebrates appeared to be slightly more common during the late season (September – October) than the early season (July – August) across years. Anchovy prey exhibited similar incidence levels between seasons (Fig. 2.5). In 2004 bottom trawl samples, butterfish were relatively common (c. 40% incidence) during the early season in 2004 (Fig. 2.5). Further, silversides were slightly more common during the early season across years. The only evidence of cannibalism in the entire study occurred during the month of August in 2004.

The diet composition of bluefish collected in shoal (5 – 9 m) and deep (9 – 18 m) waters in the coastal ocean was similar. No significant differences of incidence of any prey type were detected between depth strata using either mid-water trawl data (pooled across years) (Fig. 2.6) or 2004 bottom trawl data (Fig. 2.6). Sciaenids were not a common prey item, yet when present they only occurred in bluefish collected from shoal waters, irrespective of gear type. Butterfish were more common in deep (c. 40% incidence) than shoal (< 10% incidence) waters based on bottom trawl data (Fig. 2.6).

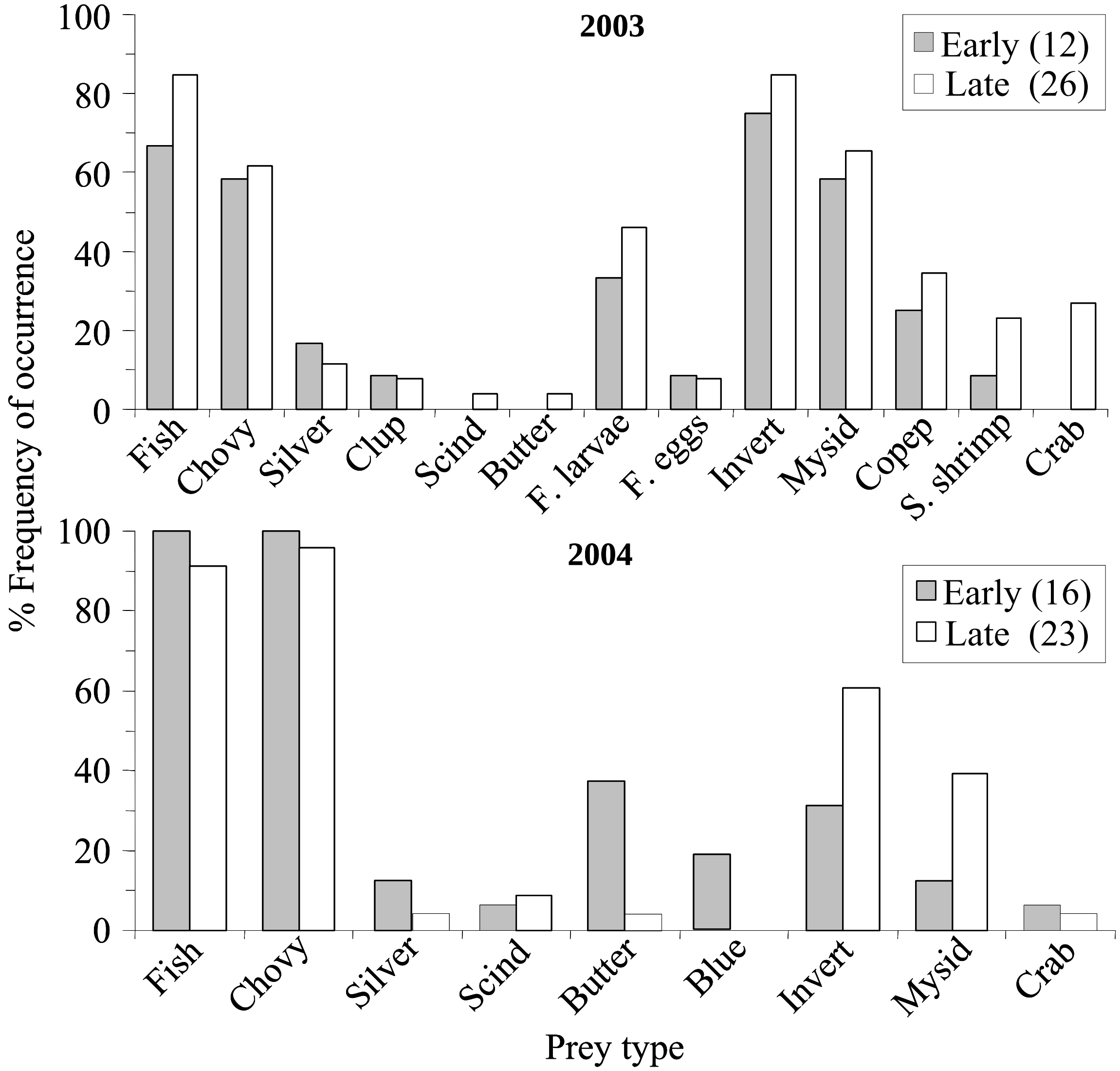


Figure 2.5. Seasonal diet composition of juvenile bluefish collected during 2003 in Maryland coastal waters with mid-water trawl. %FO reported as the percent of tows from which one or more bluefish guts contained a particular prey type. Total number of tows with bluefish each season is given parenthetically. No significant differences in %FO for any prey type between early (July, August) and late (September, October) seasons. Fish = total fish, chovy = anchovy, silver = silverside, clup = clupeid, scind = sciaenid, butter = butterfish, f. larvae = fish larvae, f. eggs = fish eggs, invert = total invert, mysid = mysid shrimp, copep = calanoid copepod, s. shrimp = sand shrimp, and crab = crab megalopae.

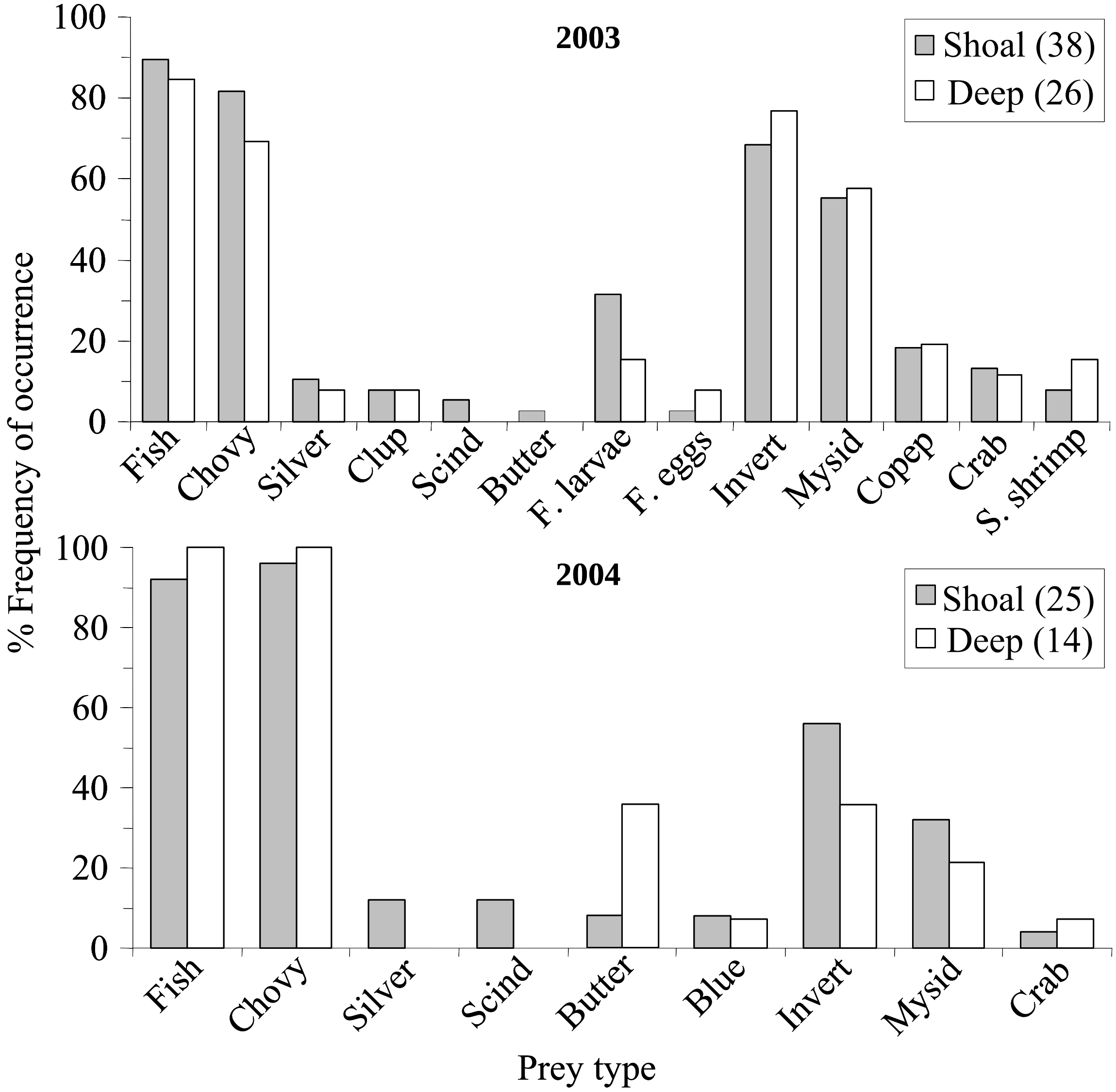


Figure 2.6. Diet composition of juvenile bluefish collected in shoal ($\leq$ 10 m) and deep (10 – 18 m) waters in the coastal ocean. Diet data pooled across years 2000, 2001, and 2003. Mid-water trawl employed for collections. %FO reported as the percent of tows from which one or more bluefish guts contained a particular prey type. Total number of tows with bluefish in each depth stratum is given parenthetically. No significant differences in % FO for any prey type between depth strata. Fish = total fish, chovy = anchovy, silver = silverside, clup = clupeid, scind = sciaenid, butter = butterfish, f. larvae = fish larvae, f. eggs = fish eggs, invert = total invert, mysid = mysid shrimp, copep = calanoid copepod, s. shrimp = sand shrimp, and crab = crab megalopae.

During 2004, silversides were only present in guts of bluefish collected in shoal waters, and were slightly more common in shoal v. deep waters in mid-water trawl samples. Incidence of anchovy prey was marginally higher in shoal v. deep waters for bluefish collected by mid-water trawl, and approximately equal between depth strata for bluefish collected by bottom trawl. Invertebrates exhibited higher incidence in shoal v. deep waters, based on mid-water trawl data; the converse was true for YOY bluefish collected via bottom trawl.

Diets of YOY bluefish differed between spring and summer cohorts in 2003 (Fig. 2.7). The %FO of fish prey was significantly higher (sampling unit = individual fish for this analysis) for the summer cohort ($p = 0.05$); %FO of invertebrates ($p = 0.03$) and silversides ($p = 0.05$) was significantly higher for the spring cohort. Anchovy comprised the majority of ‘fish’ prey, and appeared to be more important for the summer (c. 50% FO or %W) than the spring cohort (c. 30% FO or %W), although the difference in occurrence of anchovy between cohorts was not significant (Fig. 2.7). Mysid shrimp, sand shrimp, copepods, and polychaetes were more common for the spring cohort than the summer cohort. In 2004, no significant differences in %FO of prey existed between cohorts (Fig. 2.8). Overall, diet metrics of percent frequency of occurrence and percent by weight for respective prey items mirrored one another within each year’s sample.

### *Surf Zone*

In the limited numbers of juvenile bluefish ($n = 19$ across years) collected in exposed surf zone habitats, anchovies were the most common prey (50% FO) and most important in terms of weight (45% W); whereas mysid shrimp ranked second in terms of occurrence and weight (Table 2.5). Crab megalopae and silversides were moderately

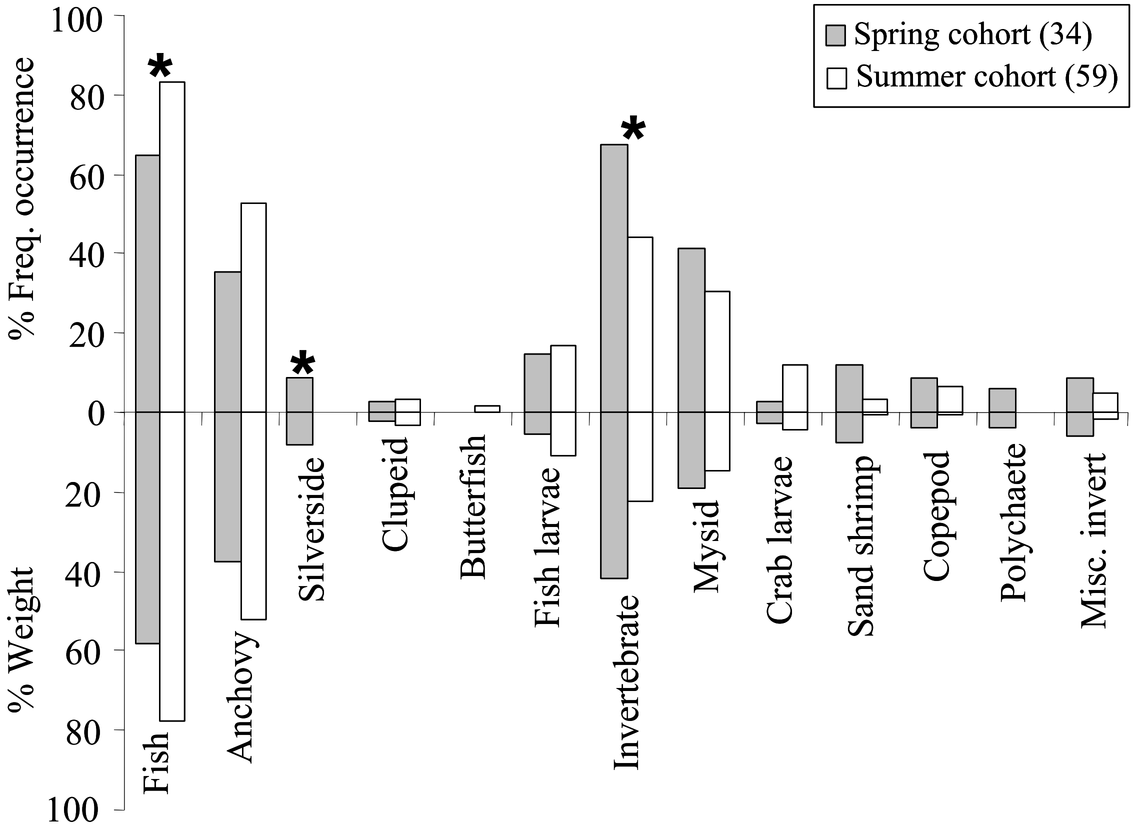


Figure 2.7. Diet composition of spring and summer cohorts of juvenile bluefish in Maryland coastal waters during 2003 (mid-water trawl). Diet data reported only for directly aged individuals, and sample sizes given parenthetically. Positive and negative ordinate axes correspond to diet indices of percent frequency of occurrence (%FO) and relative percent weight (%W), respectively. Diet indices calculated on a per fish basis (i.e. the sampling unit is an individual fish). Asterisks denote significant differences in %FO between cohorts, based on chi-square tests of independence. Misc. inverts = unidentified crustaceans for both cohorts.

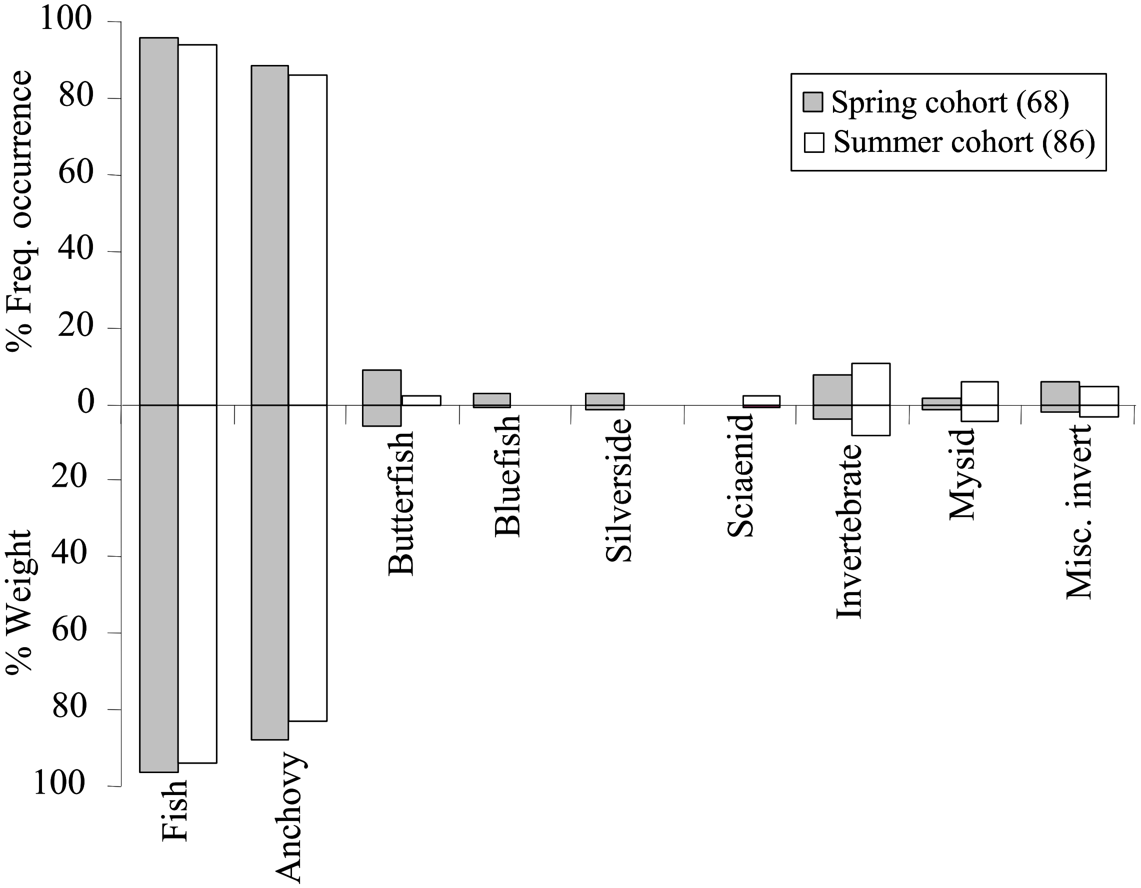


Figure 2.8. Diet composition of spring and summer cohorts of juvenile in Maryland coastal waters during 2004 (bottom trawl). Diet data reported only for directly aged individuals, and sample sizes given parenthetically. Positive and negative ordinate axes correspond to diet indices of percent frequency of occurrence (%FO) and relative percent weight (%W), respectively. Diet indices calculated on a per fish basis (i.e. the sampling unit is an individual fish). No significant differences in %FO of any prey type between cohorts.

Table 2.5. Diet composition of juvenile bluefish collected in Maryland surf zone habitats during 2000, 2001, and 2004. Percent frequency of occurrence (%FO) and relative percent weight (%W) indices calculated on a per fish basis (only individuals with food in their guts). The number of bluefish guts containing a particular prey item is given parenthetically. Debris = sand grains; %W not calculated for miscellaneous categories.

| Prey type | %FO | %W |
|---|---|---|
| FISH | 72.2 (13) | 63.6 |
| *Anchoa* sp. | 50.0 (9) | 44.8 |
| *Menidia* sp. | 16.7 (3) | 10.2 |
| UnID fish | 22.2 (4) | 8.6 |
| INVERTEBRATES | 61.1 (11) | 36.4 |
| Mysid shrimp | 33.3 (6) | 18.6 |
| Crab megalopae | 27.8(5) | 8.6 |
| Polychaete | 5.6 (1) | 0.1 |
| UnID crustacean | 22.2 (4) | 9.0 |
| MISCELLANEOUS | | |
| Debris | 5.6 (1) | |
| No. guts examined | 19 | |
| % (No.) empty | 5.3 (1) | |
| Total length (mm) range | 60 - 181 | |

common and important components of the diet; polychaetes were rare. Unidentified fish and crustacean prey were fairly common, c. 20% FO; only 1 of 19 bluefish had an empty stomach.

*Chesapeake Bay – littoral habitats*

Juvenile bluefish collected in littoral habitats (beach seine) in Chesapeake Bay were chiefly piscivorous: fish prey %FO and %W were consistently greater than 93% across five years of data (Table 2.6). Silversides were the most common (50 – 60% FO) and important (40 – 60 %W) prey across years; with anchovies generally ranking second in incidence and biomass, except in 2004 when anchovy were more common than silversides. Less common fish prey included clupeids (e.g., Atlantic menhaden, *Brevoortia tyrannus*) and moronids (e.g., striped bass, *Morone saxatilis*); uncommon fish prey included sciaenids (e.g., spot, *Leiostomus xanthurus*), which only occurred in 2004. Clupeids, moronids, and sciaenids were not consistently identified to species level, due to varying rates of digestion. Unidentified fish prey ranged from 8 – 24% FO, and 8 – 20% W across years.

Invertebrates were moderately common (0 – 21% FO across years); however, they contributed minimally to diet biomass (< 7 %W across years) (Table 2.6). Polychaetes (*Nereis sp.*) were the most common invertebrate prey; uncommon invertebrates included grass, mysid, and sand shrimp, amphipods, isopods, calanoid copepods, and crab megalopae. The percent of empty stomachs ranged from 14 – 27% across years.

Significant differences among years were detected in feeding incidence on silversides ($p = 0.001$) and moronids ($p = 0.02$) (Fig. 2.9). The difference in silverside occurrence among years was due to low incidence levels (c. 30% FO) in 2004 (Fig. 2.9).

Table 2.6. Diet composition of juvenile bluefish collected in littoral habitats of Chesapeake Bay during 1999, 2000, 2001, 2003, and 2004. Percent frequency of occurrence (%FO) and relative percent weight (%W) indices were calculated on a per fish basis (only individuals with food in their guts). The number of bluefish guts containing a particular prey is item given parenthetically in % F.O. column. *Anchoa* sp. in 2003 and 2004 were all bay anchovy, but identification of anchovy prey to species level not conducted for samples from 1999-2001. Macroalgae was generally *Ulva* sp.; seagrass (*Zostera marina*). Debris category encompasses sand grains, rock, petrified wood material, plastic, wire, and monofilament fishing line. %W was not calculated for miscellaneous categories.

| Prey type | 1999 | | 2000 | | 2001 | | 2003 | | 2004 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | % FO | %W | % FO | %W | % FO | %W | % FO | %W | % FO | %W |
| FISH | 96.9 (94) | 93.4 | 97.2 (209) | 95.8 | 97.9 (95) | 96.9 | 100 (11) | 100 | 96.1 (73) | 93.6 |
| *Menidia* sp. | 51.6 (50) | 49.3 | 57.2 (123) | 51.3 | 62.9 (61) | 61.0 | 54.5 (6) | 49.3 | 15.8 (12) | 15.0 |
| *Anchoa* sp. | 18.6 (18) | 18.5 | 18.1 (39) | 14.9 | 14.4 (14) | 14.2 | 54.5 (6) | 41.6 | 48.7 (37) | 45.1 |
| Moronidae | 2.1 (2) | 2.1 | 6.0 (13) | 5.2 | 6.2 (6) | 5.9 | | | | |
| Clupeidae | 3.1 (3) | 2.6 | 7.9 (17) | 6.4 | 2.1 (2) | 2.1 | | | 22.4 (17) | 21.7 |
| Sciaenidae | | | | | | | | | 4.0 (3) | 3.7 |
| UnID fish | 23.7 (23) | 20.4 | 24.2 (52) | 18.0 | 14.4 (14) | 13.7 | 1 (9.1) | 9.1 | 7.9 (6) | 7.9 |
| unID fish eggs | | | | | | | | | 1.3 (1) | 0.1 |
| INVERTEBRATES | 21.6 (21) | 6.6 | 8.4 (18) | 4.2 | 6.2 (6) | 3.1 | | | 17.8 (13) | 6.4 |
| Polychaete (*Nereis sp.*) | 6.2 (6) | 2.6 | 5.1 (11) | 2.4 | 3.1 (3) | 1.7 | | | 11.8 (9) | 4.7 |
| Mysid shrimp | | | 3.3. (7) | 1.8 | 1.0 (1) | 1.0 | | | | |
| *Palaemonetes* sp. | 1.0 (1) | 1.0 | | | | | | | 1.3 (1) | 0.1 |
| *Crangon* sp. | 3.1 (3) | 2.2 | | | | | | | | |
| Amphipod | 1.0 (1) | 0.02 | | | | | | | 1.3 (1) | 0.2 |
| Crab megalopae | | | | | 1.0 (1) | 0.01 | | | | |
| Calanoid copepod | | | | | | | | | 1.3 (1) | 1.3 |
| Isopod | | | | | | | | | 1.3 (1) | 0.08 |
| UnID crustacean | 8.2 (8) | 0.7 | | | 1.0 (1) | 0.3 | | | | |

Table 2.6 con't…

| Prey type | 1999 | | 2000 | | 2001 | | 2003 | | 2004 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | %FO | %W | %FO | %W | %FO | % W | %FO | %W | %FO | %W |
| MISCELLANEOUS | | | | | | | | | | |
| Debris | | | | | | | | | 7.9 (6) | |
| Macroalgae | | | | | | | | | 2.6 (2) | |
| Seagrass | | | | | | | | | 2.6 (2) | |
| | | | | | | | | | | |
| No. guts examined | 114 | | 267 | | 123 | | 15 | | 92 | |
| % (No.) empty | 14.0 (16) | | 19.9 (53) | | 21.1 (26) | | 26.7 (4) | | 17.4 (16) | |
| Total length (mm) range | 73 – 290 | | 49 – 209 | | 54 - 257 | | 120 - 179 | | 58 - 208 | |

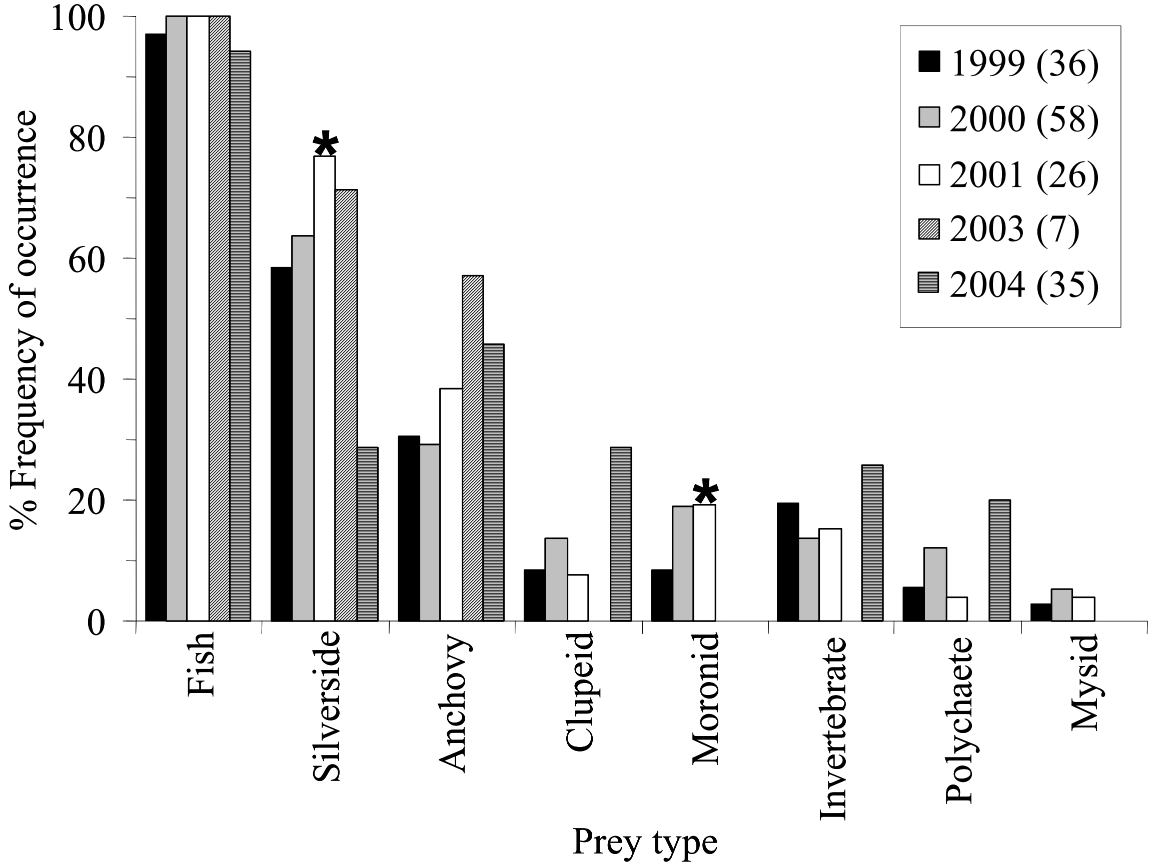


Figure 2.9. Annual diet composition of juvenile bluefish collected in littoral habitats of Chesapeake Bay (beach seine). %FO reported as the percent of tows from which one or more bluefish guts contained a particular prey type. Total number of tows with bluefish each year is given parenthetically. Asterisks denote significant differences in %FO among years for a given prey item, based on chi-square tests of independence.

Moronids were present during 1999 – 2001 (10 – 20% FO) and absent during 2003 and 2004. The most anomalous year was 2004, when the lower incidence of silverside prey was complemented by high annual incidences of anchovy (50%), clupeid (c. 30%), and invertebrate (25%) (mainly polychaetes) prey. During 2001-2003, overall diet composition of juvenile bluefish from littoral habitats was similar. Inferences in 2003 are limited due to low sample size (15 bluefish from 7 seine hauls); bluefish collected that year consumed either silversides or anchovies, in roughly equal proportions (Table 2.6).

The incidence of silverside prey was consistently higher during the early season (May – July) than the late season (August – October) (Fig. 2.10); significantly so for data pooled across years (63 and 38% FO for early and late seasons, respectively, $p = 0.005$) and for year 2000 (77% and 21% FO for early and late seasons, respectively, $p = 0.0002$). The incidence of anchovy was significantly higher during the late season in 1999 ($p = 0.02$). Nonetheless, the incidence of anchovy was not consistently higher across other years. The incidence of clupeids, moronids, invertebrates, and polychaetes was higher (but not significant) during the early season for all years except 2000, when proportions of these prey items were similar between seasons. In contrast to coastal bluefish, mysid shrimp occurred at low levels (< 6% FO) across years and were only present during the early season.

### *Chesapeake Bay – channel habitats*

Fish prey dominated the diets of juvenile bluefish collected with a mid-water trawl in channel habitats of Chesapeake Bay during 1999 and 2001 (> 90% FO and %W) (Table 2.7). Anchovy was the principal fish prey in both years, and a relatively large percent (30%) of stomachs contained unidentified fish in 2001. These unidentified fish

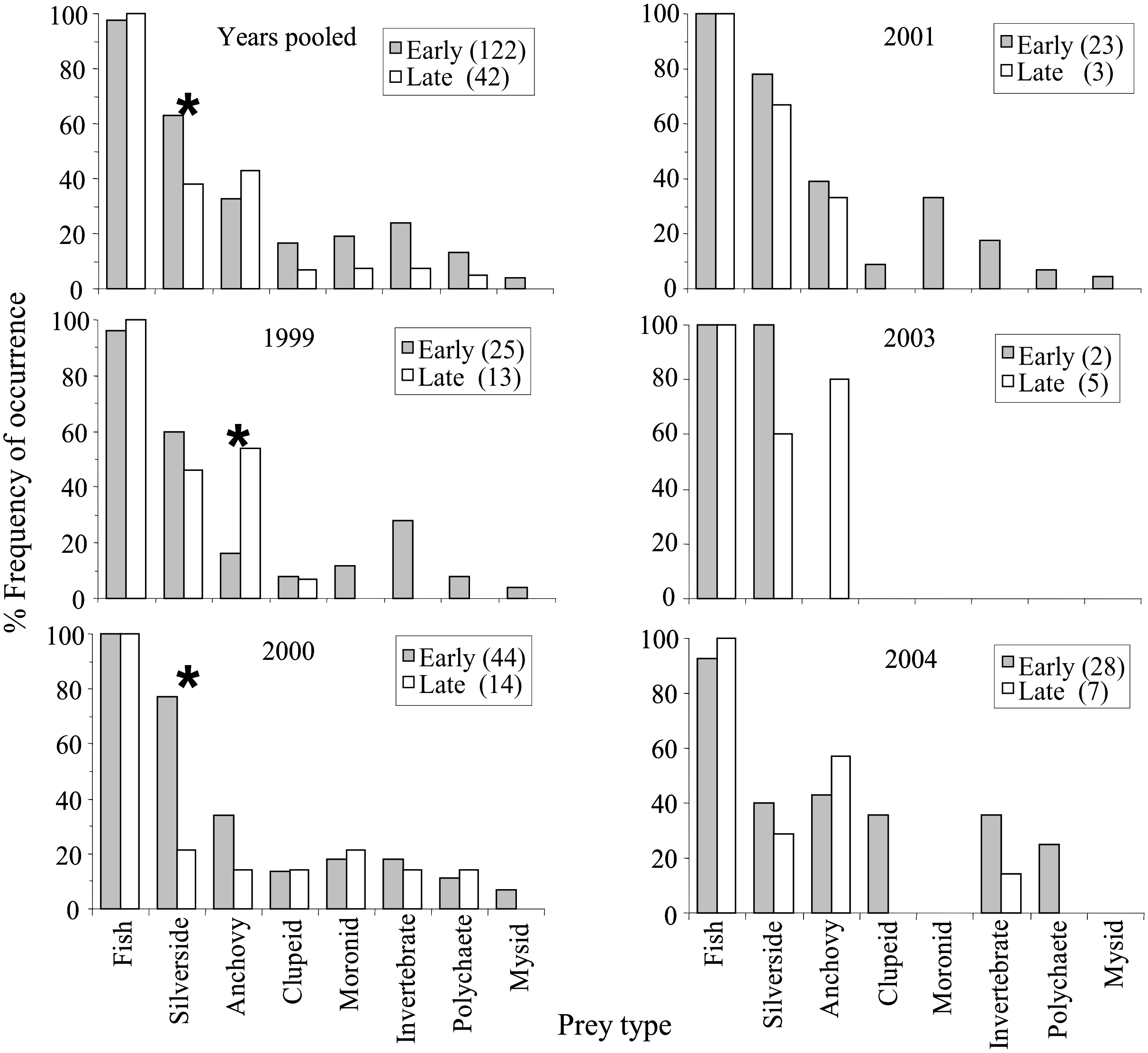


Figure 2.10. Seasonal diet composition of juvenile bluefish in littoral habitats of Chesapeake Bay during 1999 – 2004. %FO reported as the percent of tows from which one or more bluefish guts contained a particular prey type. Total number of tows with bluefish each season is given parenthetically. Asterisks denote significant differences between seasons, early (May - July) and late (August - October), for a given prey item, based on chi-square tests of independence.

Table 2.7. Diet composition of juvenile bluefish collected in mainstem regions of Chesapeake Bay during 1999, 2001, and 2004. Mid-water trawl was used for collections. Percent frequency of occurrence (%FO) and relative percent weight (%W) indices were calculated on a per fish basis (only individuals with food in their guts). The number of bluefish guts containing a particular prey item given parenthetically.

| Prey type | 1999 | | 2001 | | 2004 | |
|---|---|---|---|---|---|---|
| | %FO | %W | %FO | %W | %FO | %W |
| FISH | 100 (16) | 95.7 | 90.9 (30) | 90.9 | 40.0 (2) | 40.0 |
| *Anchoa* sp. | 93.8 (15) | 89.4 | 48.4 (16) | 46.3 | | |
| Clupeidae | | | 6.1 (2) | 6.1 | 40.0 (2) | 40.0 |
| *Menidia* sp. | | | 9.1 (3) | 9.1 | | |
| UnID fish | 12.5 (2) | 6.3 | 30.3 (10) | 29.4 | | |
| INVERTEBRATES | 6.3 (1) | 4.3 | 9.1 (3) | 9.1 | 60.0 (3) | 60.0 |
| Polychaete | | | 3.0 (1) | 3.0 | | |
| Calanoid copepod | | | | | 40.0 (2) | 40.0 |
| Caligidae copepod | | | | | 20.0 (1) | 20.0 |
| UnID crustacean | 6.3 (1) | 4.3 | 6.1 (2) | 6.1 | | |
| MISCELLANEOUS | | | | | | |
| Macroalgae | | | | | 20.0 (1) | |
| No. guts examined | 19 | | 48 | | 17 | |
| % (No.) empty guts | 15.8 (3) | | 31.3 (15) | | 70.6 (12) | |
| Total length (mm) range | 87 - 245 | | 95 – 153 | | 36 – 143 | |

were likely *Anchoa* sp. (Scott McGuire, personal communication). Invertebrates were rare in 1999 and 2001, and were mostly unidentified crustaceans (Table 2.7). The percent of empty stomachs was 16% and 31% in 1999 and 2001, respectively.

The number of bluefish with food in their stomachs was extremely low in 2004. Only 17 YOY bluefish were collected by mid-water trawl in 2004, of which 12 (71%) had empty stomachs. The majority of these individuals with empty stomachs (11/12) were < 50 mm total length (TL). The sizes of the five juveniles with food in their stomachs were 35, 46, 67, 98, and 106 mm TL. The three smallest individuals had consumed only invertebrates (calanoid and caligidae copepods); the two largest individuals had consumed only clupeids (Table 2.7). The diets of juveniles differed significantly among years (Fig. 2.11). However, these differences might be biased by the low sample size and small lengths of bluefish in 2004.

Diets of juveniles collected in shoal (5 – 10 m) and deep (10 – 40 m) waters in Chesapeake Bay were similar (Fig. 2.12). Fish prey (primarily anchovies) exhibited a higher incidence in juveniles collected in shoal (90% FO) v. deep waters (70% FO); copepods and clupeids were only present in guts of YOY bluefish collected in deep waters, yet none of these differences were significant.

The only direct comparison of diet composition of juvenile bluefish between systems (i.e., Chesapeake Bay estuary vs. Maryland coastal waters) was that utilizing diet data from mid-water trawl collections in 2001. In 2001, the incidence of invertebrate prey and mysid shrimp were significantly higher in the coastal ocean than in Chesapeake Bay ($p = 0.01$ invertebrates, $p = 0.004$ mysids). The %FO of invertebrates was 63% and 17% in the coastal ocean and Chesapeake Bay, respectively. Mysid shrimp were absent

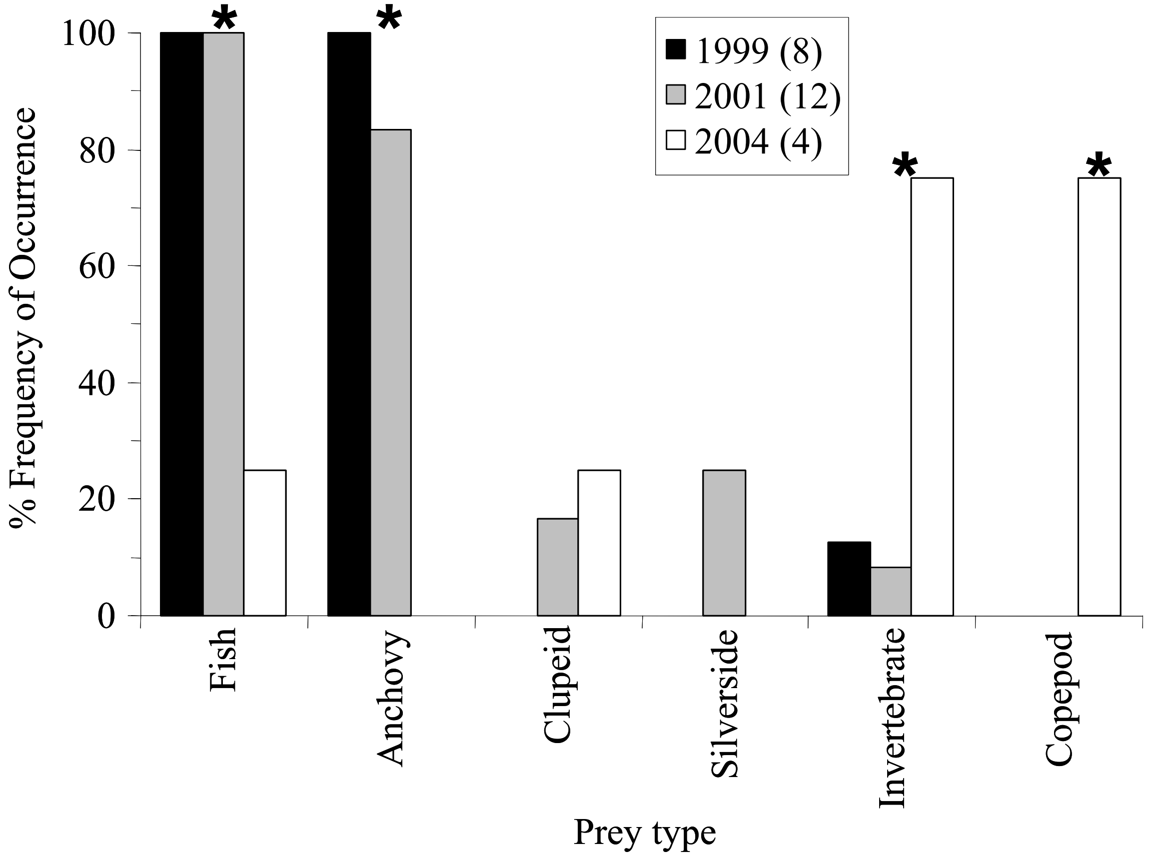


Figure 2.11. Annual diet composition of juvenile bluefish collected channel habitats of Chesapeake Bay (mid-water trawl). %FO reported as the percent of tows from which one or more bluefish guts contained a particular prey type. Total number of tows with bluefish each year is given parenthetically. Asterisks denote significant differences in %FO among years for a given prey item, based on chi-square tests of independence.

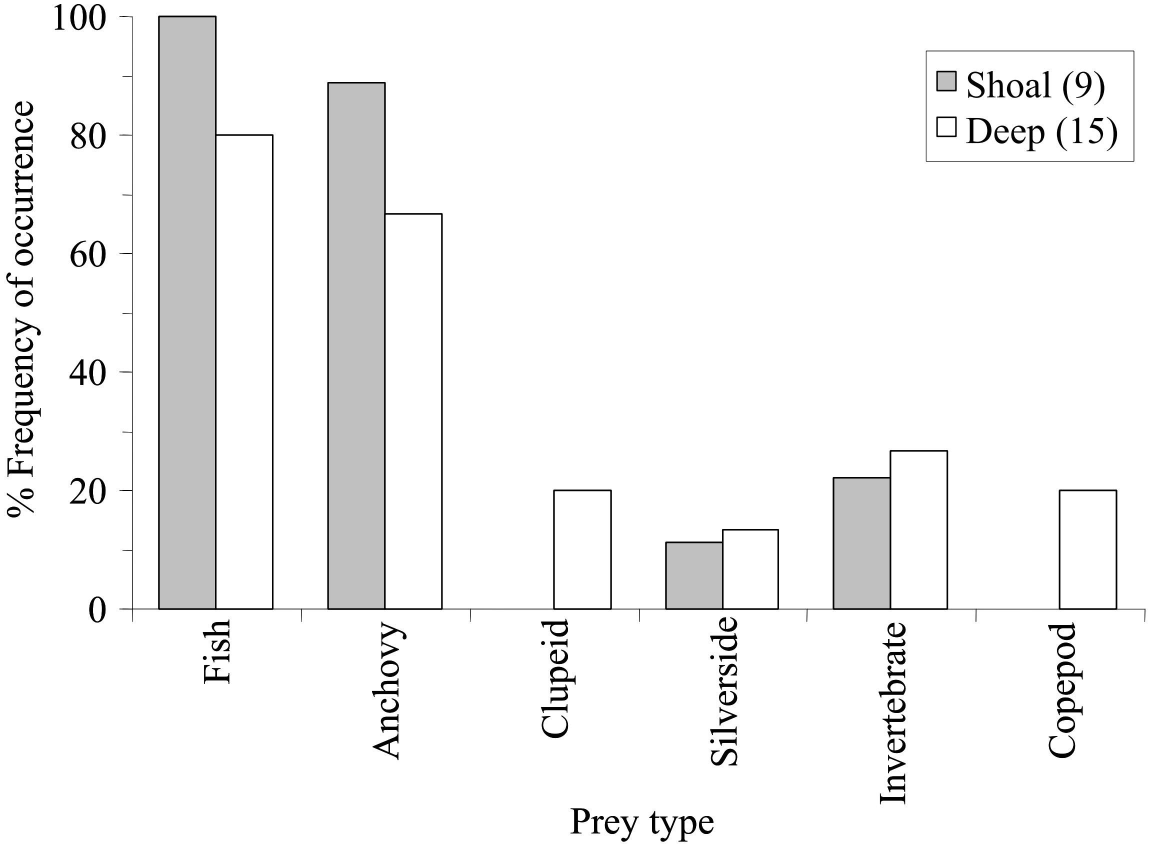


Figure 2.12. Diet composition of juvenile bluefish collected in shoal (≤ 10 m) and deep (10 – 40 m) waters in Chesapeake Bay (mid-water trawl). Data pooled across years 1999, 2001, and 2004. %FO reported as the percent of tows from which one or more bluefish guts contained a particular prey type. Total number of tows with bluefish in each depth stratum is given parenthetically. No significant differences in %FO for any prey type between depth strata.

in stomachs of YOY bluefish collected in Chesapeake Bay, whereas mysids occurred in 53% (10/19) of tows in the coastal ocean (Fig. 2.13). Incidence of fish prey was 100% in both systems; the majority of which was *Anchoa sp.*, which exhibited slightly higher occurrence in the coastal ocean (100%) than Chesapeake Bay (80%) (Fig. 2.13). Clupeids were more common in Chesapeake Bay; silversides more common in the coastal ocean. Mullets and sciaenids were rare (< 6% FO) and only present in the coastal ocean; polychaetes were present at low levels (< 8% FO) in both systems.

### *Principal Components Analyses of Diet*

Separate principal components analyses were performed for diet data collected from each system and gear type (e.g., ocean mid-water trawl samples), with data pooled across years. For coastal ocean mid-water trawl diet data, the first three eigenvalues explained 47% of the total sample variance. General categories of 'invertebrate' and 'fish' prey loaded in opposition to one another along principal component 1 (PC1) (Fig. 2.14A). The overall proximity of loadings for anchovy and 'fish' vectors as well as 'invertebrate' and mysid vectors suggests that 'fish' prey was largely composed of anchovies and 'invertebrate' prey largely composed of mysids. Individual scores for PC1 were significantly different among years ($p<0.0001$). PC1 scores in 2000 and 2001 were consistently negative, but the majority ($\geq$ 75%) of scores in 2003 were positive (Fig 2.14B). This is consistent with the observed increased importance of invertebrates in 2003 than in 2000 and 2001 (Fig. 2.4).

For 2004 coastal ocean bottom trawl diet data, the first three eigenvalues explained 51% of the total sample variance. 'Fish' and 'invertebrate' prey appeared

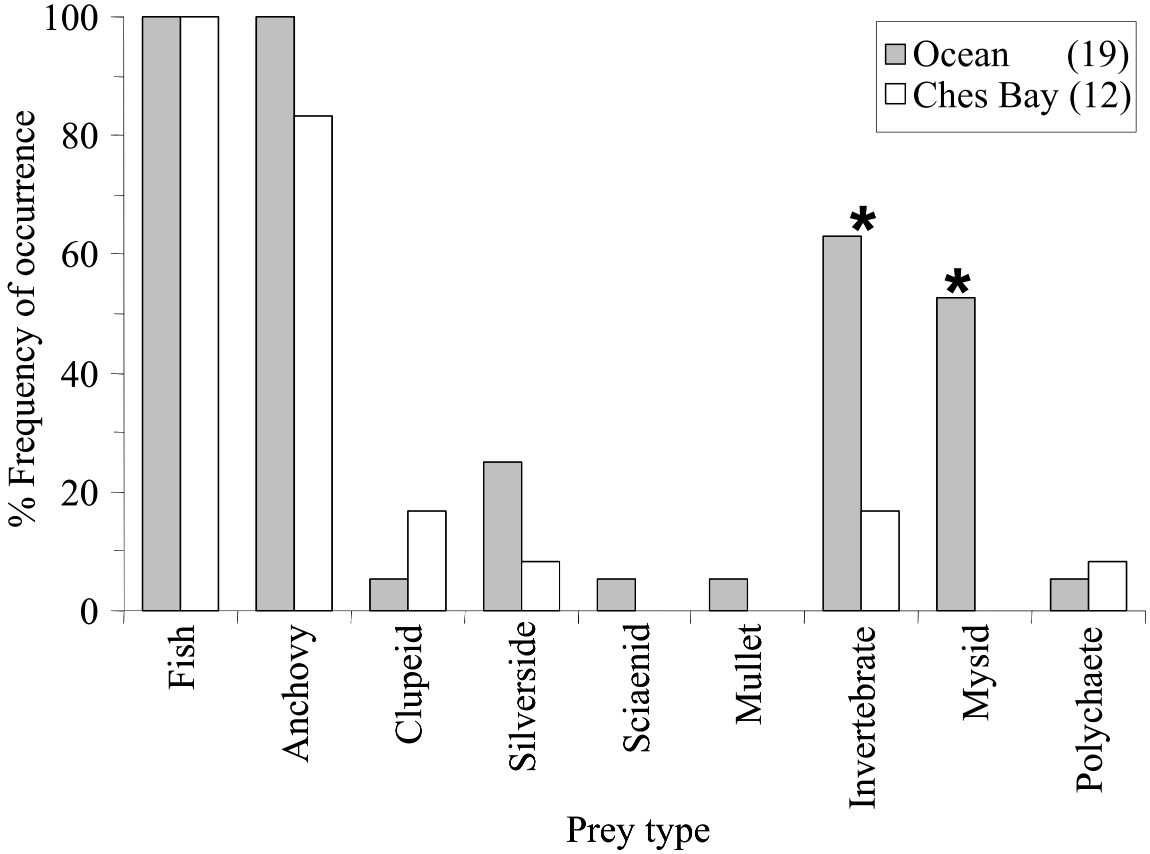
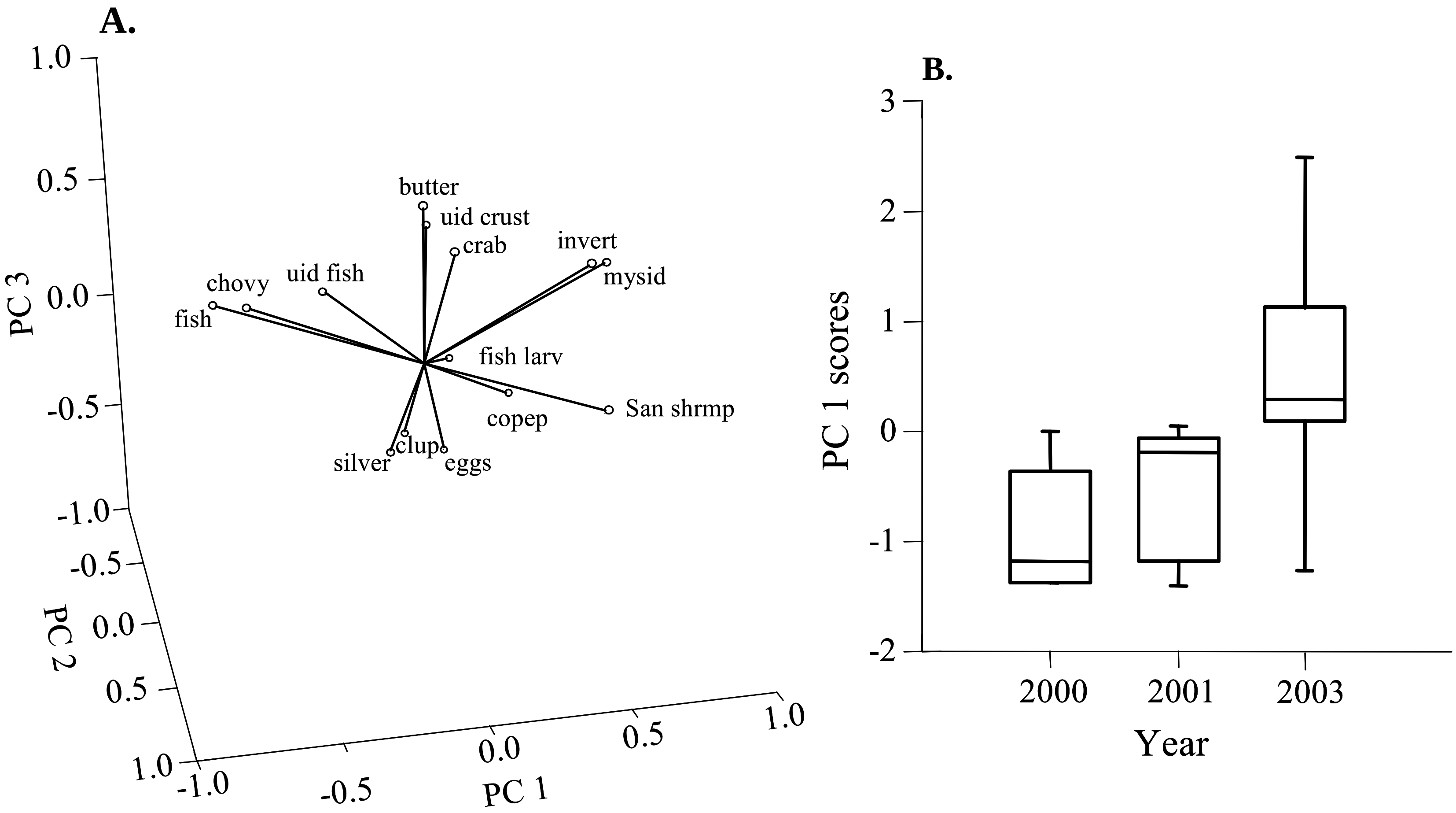


Figure 2.13. System comparison (Chesapeake Bay v. Maryland coastal waters) of diet composition of juvenile bluefish collected with mid-water trawl during 2001 in each system. %FO reported as the percent of tows from which one or more bluefish guts contained a particular prey type. Total number of tows with bluefish in each system is given parenthetically. Asterisks denote significant differences in %FO among years for a given prey item, based on chi-square tests of independence.

Figure 2.14A. Plot of loadings of variables (prey type) among the first three principal components for diet data from the coastal ocean (mid-water trawl gear). Loadings represent the correlation (Pearson's correlation coefficient) between respective principal components and the original variables. Abbreviations of prey types as follows: butter=butterfish, uid crust = unidientified crustacean, crab = crab megalopae, invert = invertebrate, mysid = mysid shrimp, san shrimp = sand shrimp, copep = copepods, eggs = fish eggs, clup = clupeids, silver = silversides, fish = fish prey, chovy = anchovies, uid fish = unidentified fish. B. Box-whisker plot of individual scores of principal component 1 by year.



again to be in opposition (PC2) with various types of fish prey (e.g., anchovy, silversides, and bluefish) and invertebrate prey (e.g., crab megalopae and snapping shrimp) showing positive and negative loadings, respectively (Fig. 2.15A). Further, squid and clams were in opposition to silversides, sciaenids, butterfish, bluefish, and unidentified fish along PC3 (Fig. 2.15A). Individual scores for PC2 were significantly different between seasons ($p = 0.04$) and depth strata ($p = 0.04$). High PC2 scores for the late season and shoal depth stratum were associated with high loadings for invertebrates, mysids, and unidentified crustaceans. Early season and the deep stratum were associated with loadings for bluefish, butterfish, and 'fish.' (Fig. 2.15B).

For Chesapeake Bay diet data from littoral habitats (seine), the first three eigenvalues explained only 38.3% of the total sample variance. In PC space, 'fish' and 'invertebrate' prey loaded in strong opposition to each other (Fig. 2.16A). The vector for the general 'fish' category stood alone (Fig. 2.16A), with no specific types of piscine prey loading with it, in contrast to observations in the coastal ocean (Figs. 2.14A, 2.15A). Individual scores on PC3 were significantly higher for the early than the late season ($p = 0.047$) and were associated with silversides and moronids in contrast to anchovy and polychaete loadings. A significant year effect was also observed ($p<0.0001$), with scores in 2004 anomalously low relative to other years, associated with anchovy and polychaete loadings (Fig. 2.16B).

For Chesapeake Bay diet data from channel habitats (mid-water trawl), the first three eigenvalues explained 82% of the total sample variance. Piscine and invertebrate prey items were again in strong opposition (PC1). Moreover, the proximity of 'fish' and anchovy vectors suggests that piscine prey were mainly anchovy. Individual scores on

Figure 2.15 A. Plot of loadings of variables (prey type) among the first three principal components for diet data from coastal ocean (bottom trawl collected, 2004). Abbreviations for prey types as follows: silver = silverside, blue = bluefish, butter = butterfish, chovy = anchovy, fish = fish prey, clams = soft-shelled clams (*Tagelus* sp.), crab = crab megalopae, snap shrimp = snapping shrimp (*Alpheus* sp.), invert = invertebrate prey, mysid = mysid shrimp, uid crust = unidentified invertebrate, uid fish = unidentified fish. B. Box-whisker plot of individual scores of principal component 2 by depth stratum (top panel) where shoal = 5 – 9 m, deep 9 – 18 m; by season, where early = July – August and late = September – November.

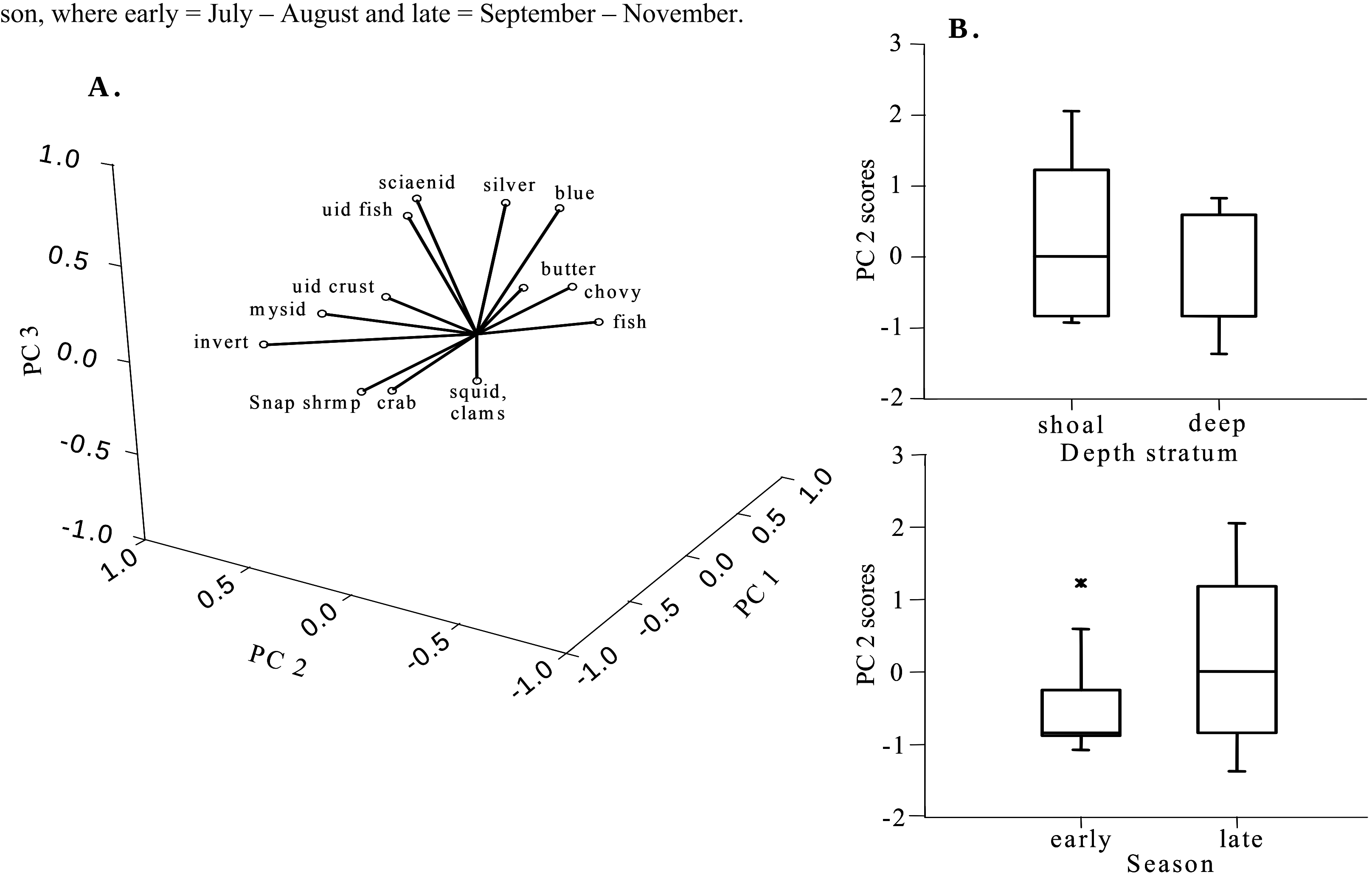
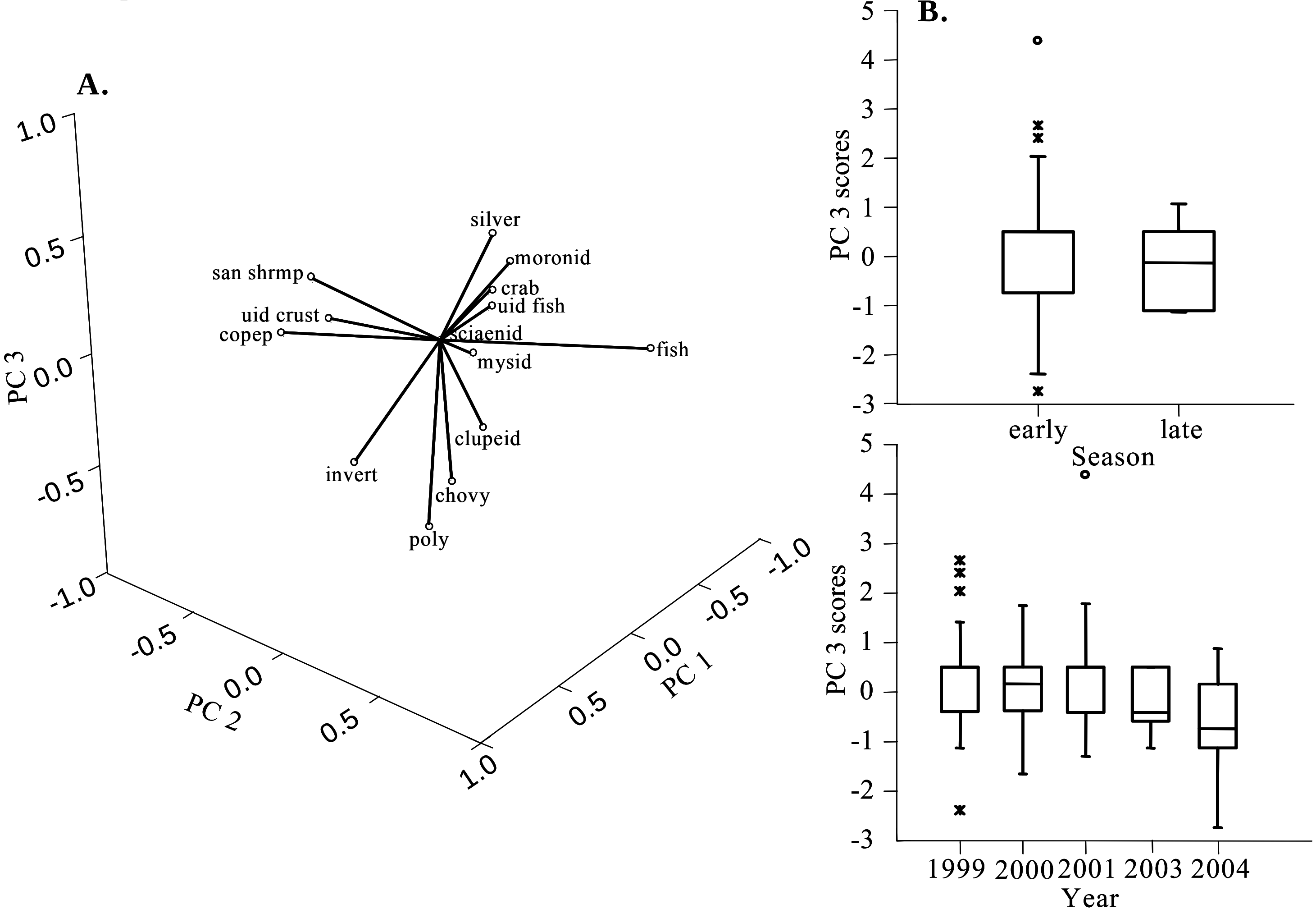


Figure 2.16 A. Plot of loadings of variables (prey type) among the first three principal components for diet data from littoral habitats (beach seine used for collections). Loadings represent the correlation (Pearson correlation coefficient) between respective principal components and the original variables. Abbreviations for prey types as follows: silver = silverside, crab = crab megalopae, uid fish = unidentified fish, fish = fish prey, mysid = mysid shrimp, chovy = anchovies, poly = polychaetes, invert = invertebrate prey, copep = calonoid copepods, uid crust = unidentified crustacean, san shrimp = sand shrimp. B. Box-whisker plot of individual scores of principal component 3 by season (top panel) where early July-August; late = September – November; by depth (bottom panel) where shoal = 5 – 9 m, deep 9 – 18 m.



PC1 were significantly different (p = 0.011) among years; scores in 1999 and 2001 were considerably higher than those in 2004 (Fig. 2.17B). As noted earlier, higher incidence of invertebrates and copepods in 2004, as shown by negative loadings here, may have been due to low sample size and smaller YOY bluefish lengths in comparison with other years.

### *Size Effects on Piscivory*

Relatively small YOY bluefish (< 100 mm total length) exhibited a similar degree of piscivory as did larger YOY (101 – 290 mm total length), irrespective of system or gear type (Table 2.8). The only test scenario (specific system and gear) that yielded a significant difference in the incidence of piscivory was for Chesapeake Bay channel habitats (mid-water trawl data), where the incidence of piscivory was significantly higher for large (94%) than for small (40%) YOY. Nevertheless, this particular comparison may not be representative of size-associated differences in piscivory because only five individuals were included in the "small" group.

Piscivory was also examined among more finely scaled size bins (40 mm) to discern potential ontogenetic (i.e., size) patterns of feeding on piscine and/or invertebrate prey. Significant differences in the incidence of piscivory were observed among size bins for mid-water trawl data collected in both the coastal ocean and Chesapeake Bay (Fig. 2.18), where YOY <80 mm showed a lower incidence of piscivory than at larger sizes. Further, a significant difference in feeding incidence on invertebrates among sizes was detected for Chesapeake Bay, where YOY < 80 mm showed higher incidence of invertebrates in stomachs than at larger sizes. Regardless of system or gear type, juvenile

Figure 2.17 A. Plot of loadings of variables (prey type) among the first three principal components for diet data from channel habitats in Chesapeake Bay (mid-water trawl gear). Loadings represent the correlation (Pearson correlation coefficients) between respective principal components and the original variables. Abbreviations for prey types as follows: silver = silverside, crab = crab megalopae, uid fish = unidentified fish, fish = fish prey, mysid = mysid shrimp, chovy = anchovies, poly = polychaetes, invert = invertebrate prey, copep = calonoid copepods, uid crust = unidentified crustacean, san shrimp = sand shrimp. B. Box-whisker plot of individual scores of principal component 1 by year.

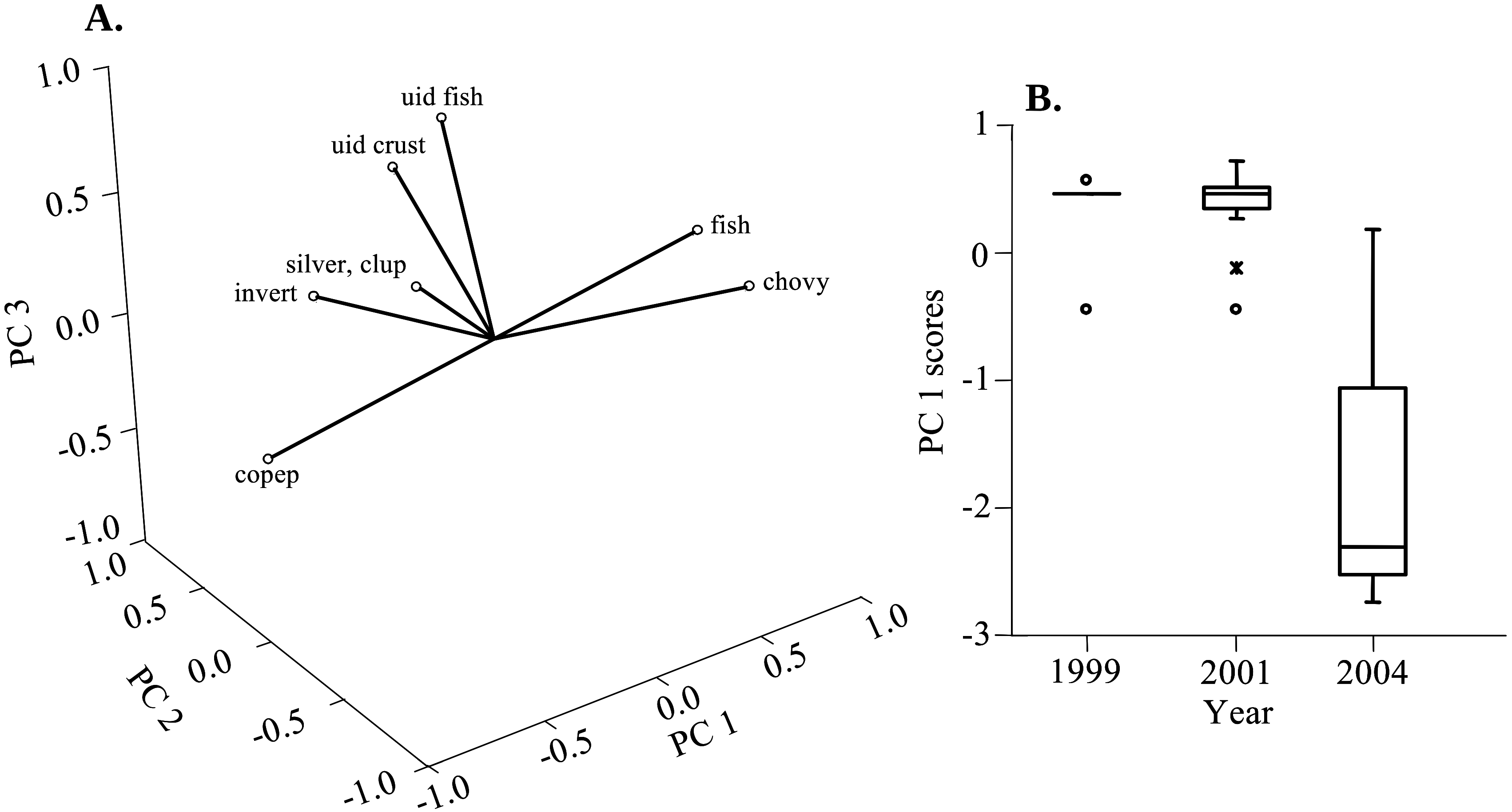


Table 2.8. Comparisons of piscivory between two broad size classes: small (< 100 mm) and large (young-of-the-year of all sizes > 100 mm) of juvenile bluefish. P-values are reported for differences in the incidence of piscivory between sizes. Comparisons were restricted to specific system/gear combinations; data was pooled across years. Parenthetic values are percent incidence of piscivory. MWT = mid-water trawl; BTrawl = bottom trawl.

| System | Gear | Size range (TL, mm) | | % Piscivory | | p value |
|---|---|---|---|---|---|---|
| | | Small | Large | Small | Large | |
| Coastal Ocean | MWT | 75 – 100 | 101 – 290 | 68% (21/31) | 74% (150/204) | 0.5 |
| Coastal Ocean | BTrawl | 68 – 100 | 101 – 200 | 92% (34/37) | 96% (296/308) | 0.4 |
| Chesapeake Bay | MWT | 35 - 98 | 105 - 245 | 40% (2/5) | 94% (6/49) | 0.0074 |
| Chesapeake Bay | Seine | 49 - 80 | 81 - 290 | 97% (85/88) | 98% (398/408) | 0.7 |

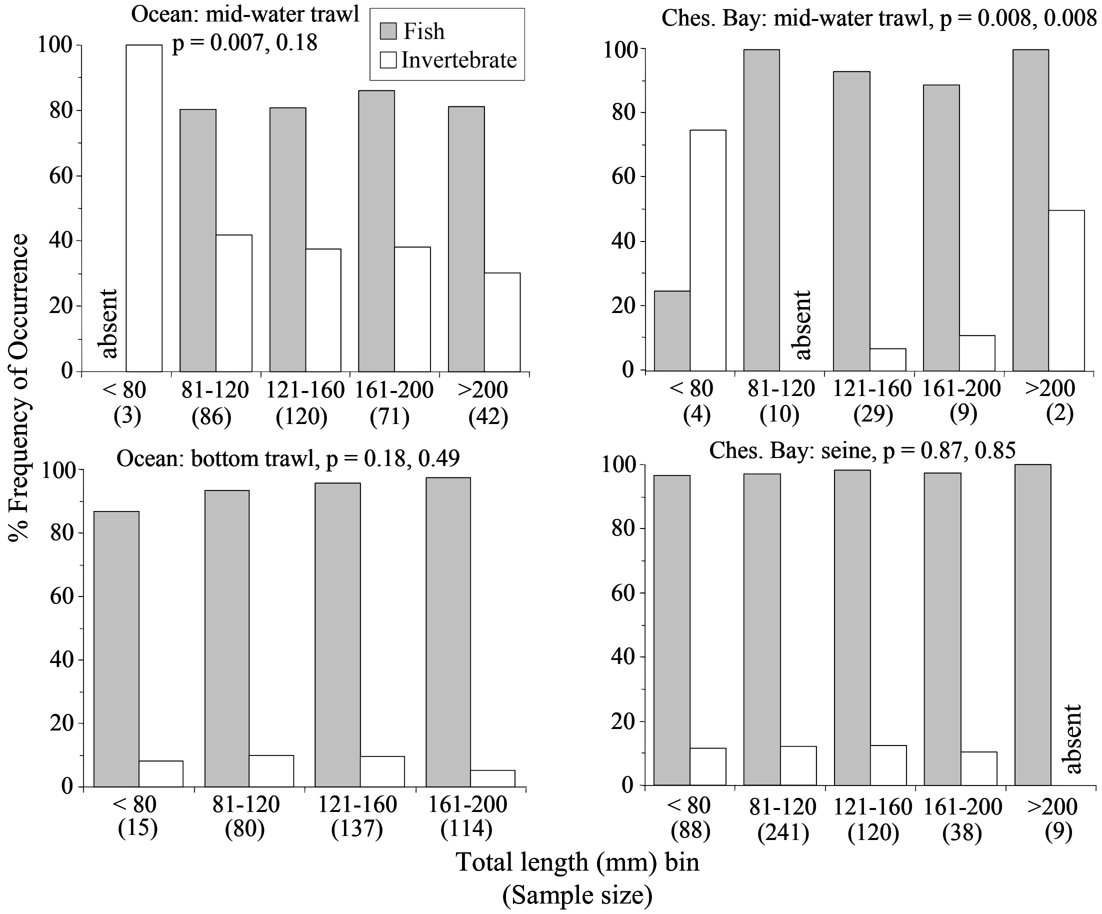


Figure 2.18. Ontogenetic diet trends of juvenile bluefish foraging on fish and invertebrate prey. Diet data pooled across years within each gear/habitat. Percent frequency of occurrence of fish and/or invertebrate prey reported on an individual basis; sample sizes for each length bin given parenthetically below bin label. P-values for chi-square tests of independence reported for each system/habitat.

bluefish > 80 mm exhibited somewhat constant levels of piscivory and feeding on invertebrates among size classes (Fig. 2.18). Incidence of piscivory was high, ranging from 80 – 100%; whereas incidence of feeding on invertebrates was typically c. 10%, except for mid-water trawl data from the coastal ocean, which indicated c. 30% incidence among all sizes of bluefish.

### *Predator-Prey Size Relationships*

A weak but significantly positive ($p = 0.01$) and linear relationship was detected between bay anchovy prey size and size of YOY bluefish, based on data from the coastal ocean during 2003 and 2004 (Fig. 2.19). The largest bay anchovy (60 – 90 mm TL) were only consumed by relatively large juvenile bluefish (> 150 mm TL), but juvenile bluefish of all sizes consistently consumed small bay anchovy (40 – 60 mm TL) (Fig. 2.19). The mean prey-predator total length ratio (PPTLR) at which juvenile bluefish consumed their prey whole ($0.29 \pm 0.012$ SE) was the same as the mean PPTLR at which prey were recovered in pieces ($0.29 \pm 0.010$ SE) (ANOVA, $p = 0.60$). The recovery of prey in pieces is likely a result of bluefish slicing prey before consumption. Although at the smallest (0.20) and largest (0.50) PPTLR's, bluefish primarily consumed prey in whole and partial form, respectively (Fig. 2.20), no consistent differences in foraging mode were observed for PPTLR's ranging from 0.2 – 0.45.

For three of four cruises in the coastal ocean, respective medians of length frequency distributions of bay anchovy recovered in guts were significantly lower than those of field-collected bay anchovy (based on median tests) (Fig. 2.21). No significant difference in field v. gut lengths of prey was observed for the July 2004 cruise, however

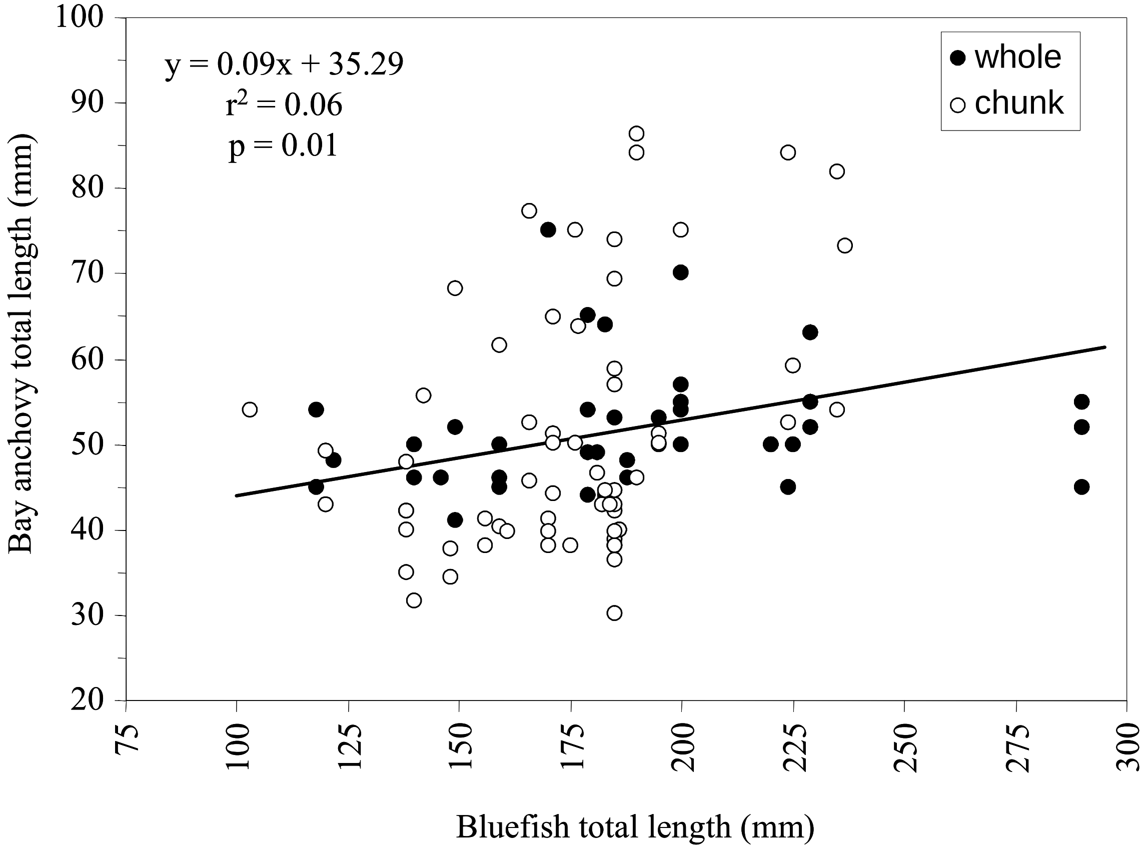


Figure 2.19. Predator-prey length relationship for juvenile bluefish predators and their primary prey, bay anchovy. Data from trawl collections in Maryland coastal waters, pooled across years 2003 and 2004. ‘Whole’ lengths (filled circles) correspond to lengths of bay anchovy prey specimens recovered in whole form, enabling direct total length measurements; when prey were recovered in ‘chunks’, original total lengths of prey were estimated using regression equations relating caudal peduncle height and eye diameter to prey total length.

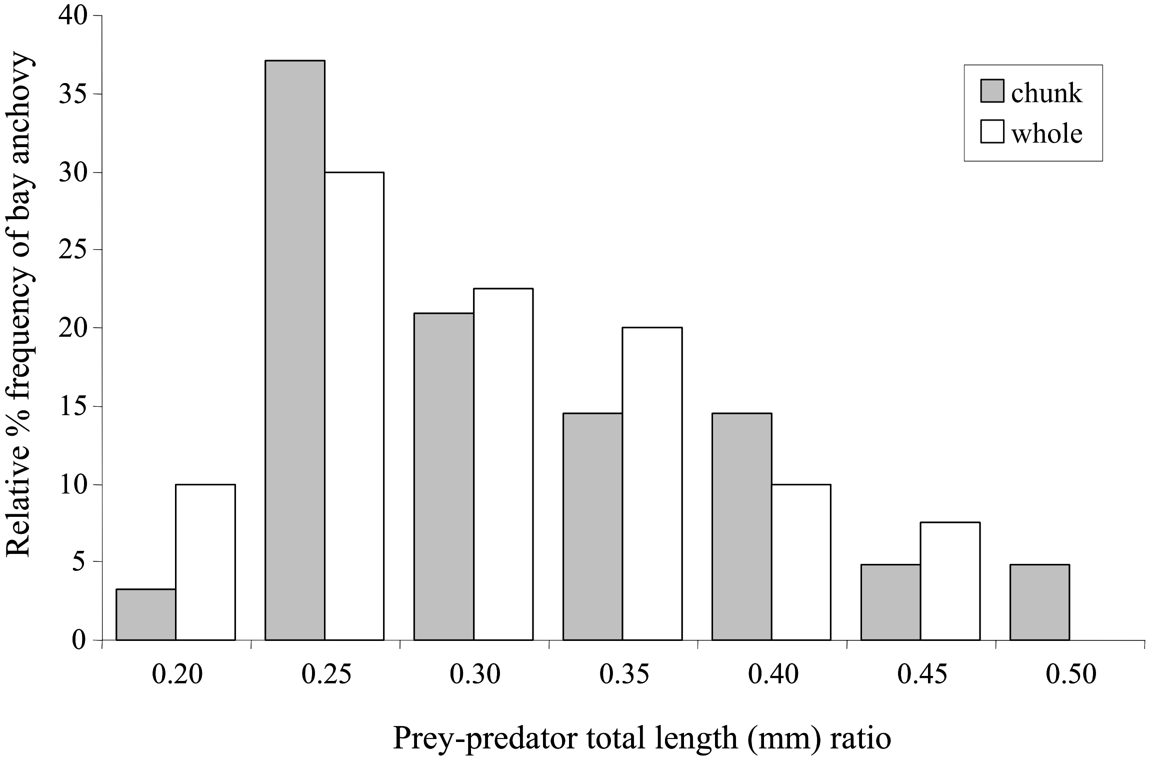


Figure 2.20. Distribution of prey-predator total length ratios for bay anchovy and juvenile bluefish. Data from trawl collections in the coastal ocean during 2003 and 2004 (pooled across years).

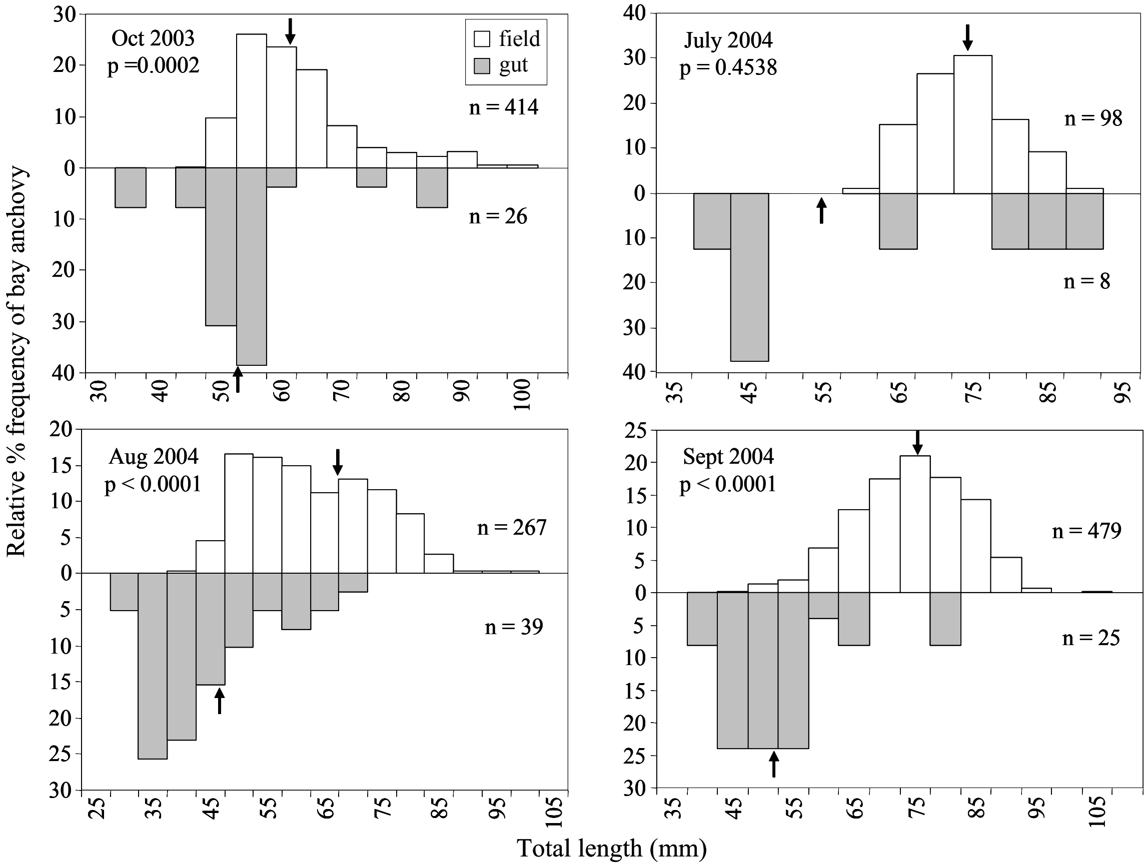


Figure 2.21. Length frequency distributions of field v. ingested total lengths of bay anchovy prey for particular cruises in Maryland coastal waters during 2003 (mid-water trawl) and 2004 (bottom trawl). n indicates sample size; data pooled across stations/days/depth strata for each cruise. Arrows indicate medians; median test (associated p-values reported) employed to compare field v. gut length distributions of bay anchovy for each cruise.

low sample size (n = 8 gut lengths) may have precluded a valid comparison for this cruise. The medians of lengths of bay anchovy consumed by juvenile bluefish were consistently c. 50 mm across cruises. Interestingly, for respective cruises, the average PPTLR's of field-collected bay anchovy versus field-collected bluefish (Table 2.9) were well within the reported range for which bluefish exhibit a high capture success (0.3 – 0.5, Scharf et al. 2002); hence, bluefish appear to have selected small bay anchovy.

## Abundance/Occurrence Analyses of YOY Bluefish and Bay Anchovy

### *System Effects*

Mean relative abundance (CPUE = catch-per-tow) of YOY bluefish was consistently higher in Maryland coastal waters than channel regions of Chesapeake Bay across years 2000, 2001, and 2003 (Fig. 2.22). CPUE in Chesapeake Bay was < 0.5 YOY bluefish tow$^{-1}$ across years; whereas CPUE in Maryland coastal waters was c. 2 and 3 bluefish tow$^{-1}$ in 2000 and 2003, respectively; and 13 bluefish tow$^{-1}$ in 2001. A two-way logistic regression model indicated that annual incidence was significantly higher in Maryland coastal waters than Chesapeake Bay ($p < 0.0001$). The interaction term (system*year) was not significant, indicating that bluefish incidence was significantly higher in Maryland coastal waters regardless of year. Diagnostic statistics (McFadden $r^2$) for the logistic model indicated a marginal fit. Therefore, I used a chi-square test of independence as an alternative test to compare bluefish incidence between systems for data pooled across years. This test detected higher annual incidence values in the coastal ocean (51% or 65/128 positive tows) than Chesapeake Bay (11% or 39/355 tows) ($p< 0.0001$).

Table 2.9. Mean total lengths (mm) (± standard errors) of YOY bluefish, bay anchovy, and striped anchovy per cruise in Maryland coastal waters during 2000, 2001, 2003, and 2004. Mid-water trawl was used for collections in 2000, 2001, 2003; bottom trawl was used in 2004. Predator-prey-total length ratios (PPTLR) represents average percent bay or striped anchovy total length to bluefish total length.

| Cruise Date | Bay anchovy TL | YOY bluefish TL | %PPTLR | Striped anchovy | %PPTLR |
|---|---|---|---|---|---|
| August 10, 11 | 55 ± 0.7 | 122 ± 6.1 | 45 | 82 ± 1.7 | 67 |
| September 21, 22 | 59 ± 0.3 | 181 ± 13.7 | 33 | 121 ± 1.3 | 67 |
| | | | | | |
| August 15, 16 | 58 ± 0.8 | 156 ± 1.6 | 37 | 104 ± 2.4 | 67 |
| September 13 | 56 ± 0.5 | 141 ± 3.7 | 40 | 98 ± 1.1 | 70 |
| | | | | | |
| July 8, 9 | 74 ± 0.4 | 105 ± 3.6 | 70 | 115 ± 0.6 | 110 |
| July 29, 30 | 71 ± 2.5 | 118 ± 2.6 | 60 | 60 ± 1.0 | 51 |
| August 19, 20 | 68 ± 1.2 | 152 ± 5.2 | 45 | 76 ± 0.9 | 50 |
| September 24, 25 | 59 ± 0.5 | 134 ± 4.9 | 44 | 102 ± 0.8 | 76 |
| October 14 | 61 ± 0.5 | 173 ± 4.1 | 35 | 117 ± 6.0 | 67 |
| | | | | | |
| July 25, 27 | 72 ± 0.6 | 139 ± 2.5 | 51 | 121 ± 1.2 | 87 |
| August 23, 24 | 66 ± 0.7 | 153 ± 1.1 | 43 | 116 ± 1.0 | 76 |
| September 22, 23 | 73 ± 0.4 | 167 ± 1.5 | 43 | 125 ± 0.4 | 75 |
| November 1, 4 | 80 ± 0.6 | 207 ± 3.8 | 39 | N/A | |

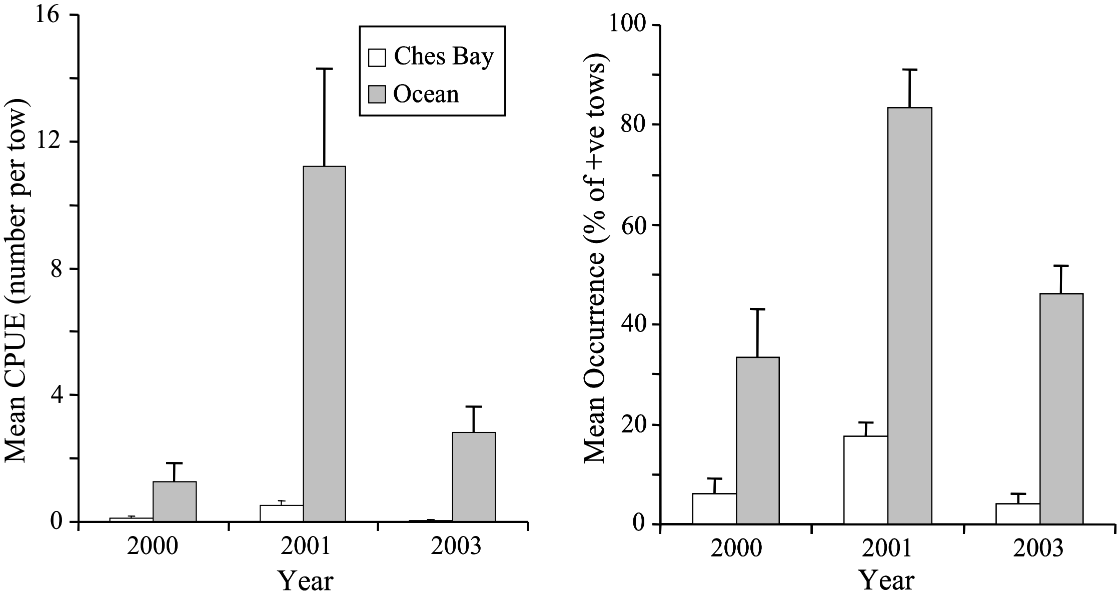


Figure 2.22. Mean annual relative abundance (left panel) and mean annual occurrence (right panel) of juvenile bluefish in Maryland coastal waters and Chesapeake Bay. Annual abundance/occurrence metrics based on mid-water trawl sampling during July-October in each system across years.

Catches of bay anchovy in Chesapeake Bay were typically higher than those in Maryland coastal waters across years, with the exception of 2000, when similar catch distributions were observed (Fig. 2.23). Bay anchovy catch data from each system were not censored by size, because across systems and years, the average PPTLR's were similar in range to those where high capture success has been reported (0.3 – 0.5, Scharf et al. 2002) (Tables 2.9, 2.10). Catches in Maryland coastal waters during 2001 and 2003 were on the order of 100's per tow, and in 2000, 1000's per tow were commonly observed (75% of tows) (Fig. 2.23). Catches in Chesapeake Bay showed much higher variability, with annual median catches c. 500 – 1000 $tow^{-1}$ and catch levels of 1000's $tow^{-1}$ common and 10,000's $tow^{-1}$ moderately common (Fig. 2.23). The Scheirer-Ray Hare extension of the Kruskal-Wallis test indicated that annual abundance of bay anchovy was significantly higher in Chesapeake Bay than Maryland coastal waters ($H = 18.36$, $p < 0.0001$). The interaction term in this model (system x year) was not significant ($H = 3.28$, $0.05 < p < 0.10$).

In contrast to bay anchovy, catches of striped anchovy were significantly higher in Maryland coastal waters than Chesapeake Bay (Fig. 2.24; chi-square test of independence for occurrence data, $p = 0.0001$). Striped anchovy were absent from upper Chesapeake Bay ($38^o$ 45'N – $39^o$ 25'N) in all years; hence, only catch data from mid- ($37^o$ 55'N - $38^o$ 45'N) and lower ($37^o$ 05'N – $37^o$ 55'N) Chesapeake Bay were utilized for abundance comparisons between systems. Mean annual occurrence values of striped anchovy in Maryland coastal waters were 75, 79, and 46% in 2000, 2001, and 2003, respectively. Mean annual occurrence levels in Chesapeake Bay were 32, 60, and 23% for the same years. Median catches in Maryland coastal waters were < 10 $tow^{-1}$ across

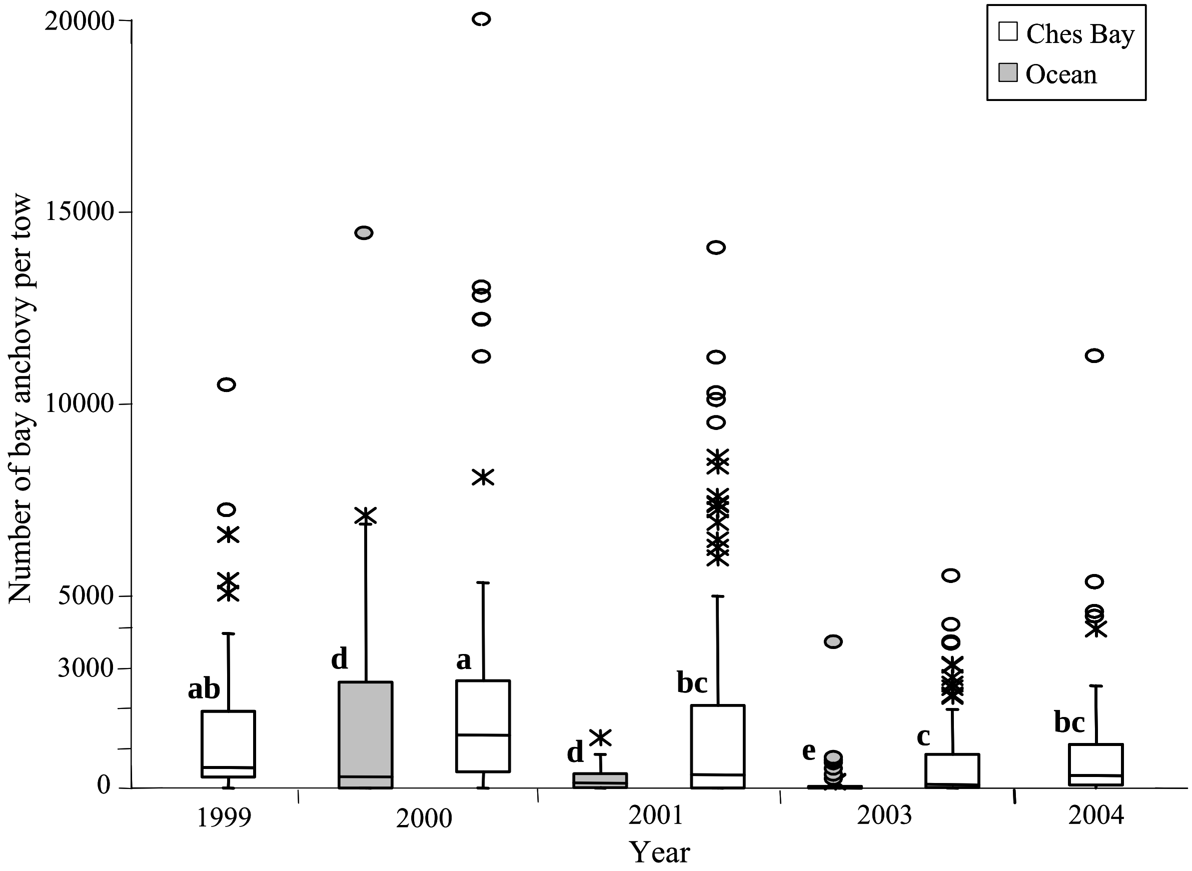


Figure 2.23. Box whisker plots of annual bay anchovy catches in Maryland coastal waters (2000, 2001, 2003) and Chesapeake Bay (1999-2001, 2003-2004). Data based on mid-water trawl sampling during July-October in each system across years. Respective system/year catch distributions with any identical letters are not significantly different among years within each system (Kruskal-Wallis test with post-hoc nonparametric Tukey type multiple comparisons) or between systems (2-way nonparametric ANOVA). Note comparisons of catches between systems only performed for 2000, 2001, and 2003; years when concurrent mid-water trawl sampling occurred in both systems.

Table 2.10. Mean total lengths (mm) (± standard errors) of YOY bluefish, bay anchovy, and striped anchovy per cruise in Chesapeake Bay (mid-water trawl) from 1999 – 2001 and 2003 – 2004. Predator-prey-total length ratios (PPTLR) represents average percent bay or striped anchovy total length to bluefish total length.

| Cruise Date | Bay anchovy TL | YOY bluefish TL | %PPTLR | Striped anchovy TL | %PPTLR |
|---|---|---|---|---|---|
| 1999 | | | | | |
| July 7 – 17 | 54 ± 0.7 | 151 ± 13.6 | 36 | N/A | |
| October 23 - 27 | 55 ± 0.4 | 173 ± 10.0 | 32 | 119 ± 0.9 | 69 |
| 2000 | | | | | |
| July 25 – 29 | 37 ± 0.2 | N/A | | 49 ± 1.0 | |
| October 17 – 21 | 50 ± 0.4 | 201 ± 31.2 | 25 | 65 ± 3.3 | 32 |
| 2001 | | | | | |
| July 6 – 14 | 38 ± 0.3 | 169 ± 3.5 | 22 | N/A | |
| July 16 – 23 | 38 ± 0.2 | 134 ± 2.3 | 28 | 45 ± 0.7 | 34 |
| September 25 – 29 | 47 ± 0.2 | 125 ± 3.9 | 38 | 94 ± 1.7 | 75 |
| October 17 - 21 | 49 ± 0.1 | 298 ± 11.5 | 16 | N/A | |
| 2003 | | | | | |
| July 7 – 14 | 52 ± 0.4 | 91[a] | 57 | 56 ± 1.5 | 62 |
| September 9 - 16 | 48 ± 0.1 | 256 ± 9.4 | 19 | 87 ± 2.4 | 34 |
| 2004 | | | | | |
| July 6 – 13 | 61 ± 0.2 | 90 ± 16.8 | 68 | 82 ± 3.7 | 91 |
| September 13 - 21 | 46 ± 0.2 | 81 ± 20.9 | 57 | 68 ± 0.4 | 84 |

[a] Only one YOY bluefish captured, therefore standard error could not be calculate

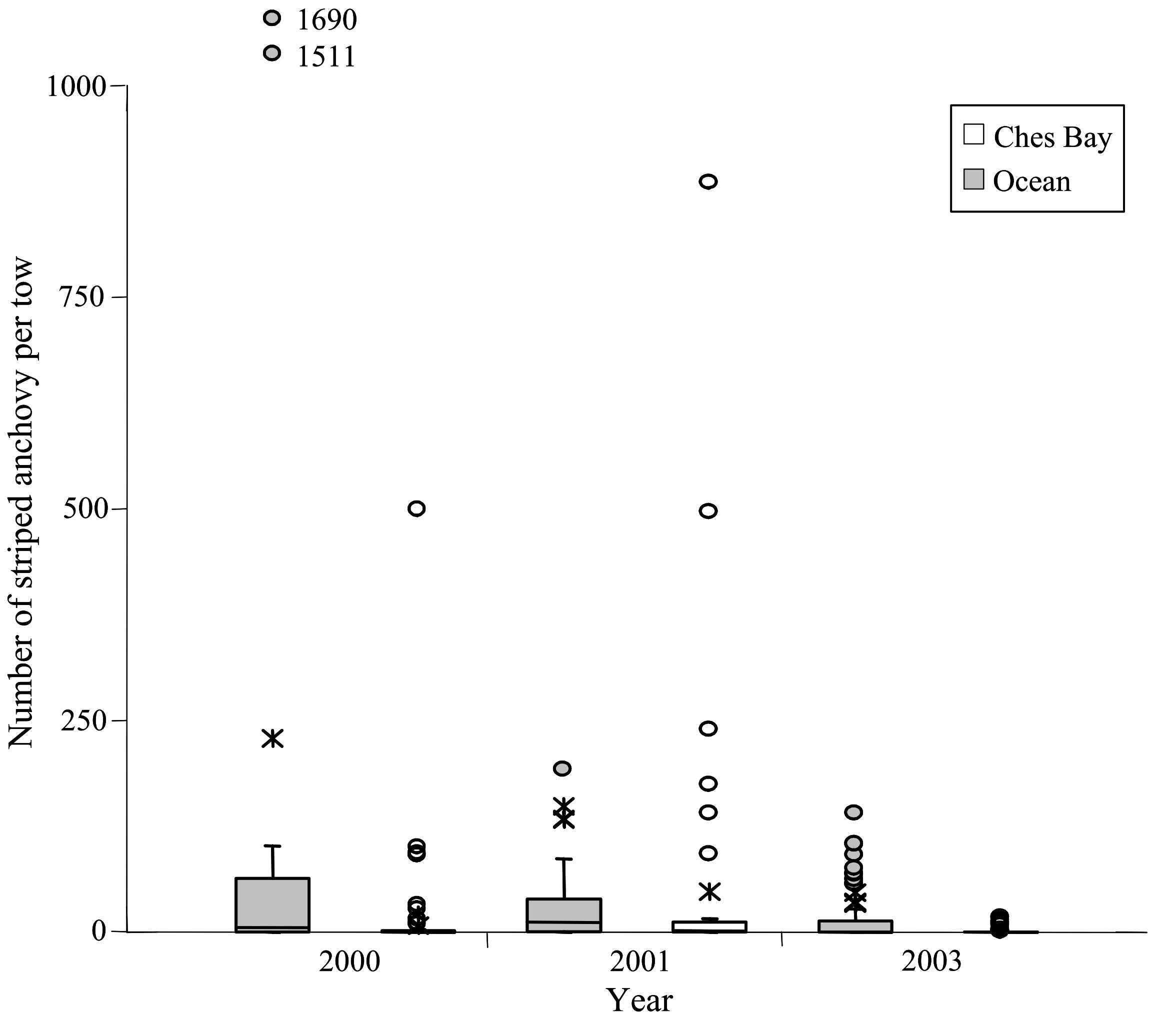


Figure 2.24. Box whisker plots of annual striped anchovy catches between systems: Maryland coastal waters v. Chesapeake Bay. Data utilized from mid-water trawl sampling during July-October in each system across years. Chesapeake Bay data includes catch data only from lower- (37o 05’N – 37o 55’N) and mid-Bay (37o 55’N - 38o 45’N). Note values reported for two outlier catches (> 1000 striped anchovy per tow) in Maryland coastal waters during 2000.

years, and the majority of individual catches were < 250 tow$^{-1}$ (Fig. 2.24). The annual abundance of striped anchovy was significantly higher in Maryland coastal waters than Chesapeake Bay (non-parametric two-way ANOVA, $H = 24.92$, $p < 0.0001$), with no significant interaction between system and year detected ($H = 2.24$, $0.1 < p < 0.25$).

For mid-water trawl catch data at individual sampling sites, bay anchovy abundances were not statistically correlated (partial $r = 0.06$, $p = 0.6$) with YOY bluefish abundances across systems (Fig. 2.25). Yet, in a coarse manner, lowest and highest abundances of either species co-occurred, but high abundances of bay anchovy were frequently observed for lowest quartile abundances of YOY bluefish.

*Interannual Comparisons – Coastal Ocean*

YOY bluefish occurrence differed significantly among years in the coastal ocean (chi-square test of independence, $p = 0.0001$). Separate chi-square tests of independence were performed to test for specific interannual differences. In paired comparisons of years, occurrence in 2001 was significantly higher than both 2000 and 2003. Indeed, mean annual occurrence was c. 2-fold higher in 2001 v. 2000 and 2003 (Fig. 2.22). Bay anchovy relative abundance differed significantly among years in the coastal ocean (non-parametric two-way ANOVA, $H = 38.22$, $p < 0.0001$). Specifically, abundance was significantly lower in 2003 v. 2000 and 2001 (based on nonparametric multiple comparisons with unequal sample sizes with Tukey-adjusted $\alpha$ values; Zar 1996) (Fig. 2.23).

*Interannual Comparions, Chesapeake Bay – channel habitats*

For interannual abundance comparisons within channel habitats of Chesapeake Bay, I incorporated two additional years of mid-water trawl data (1999 and 2004: July –

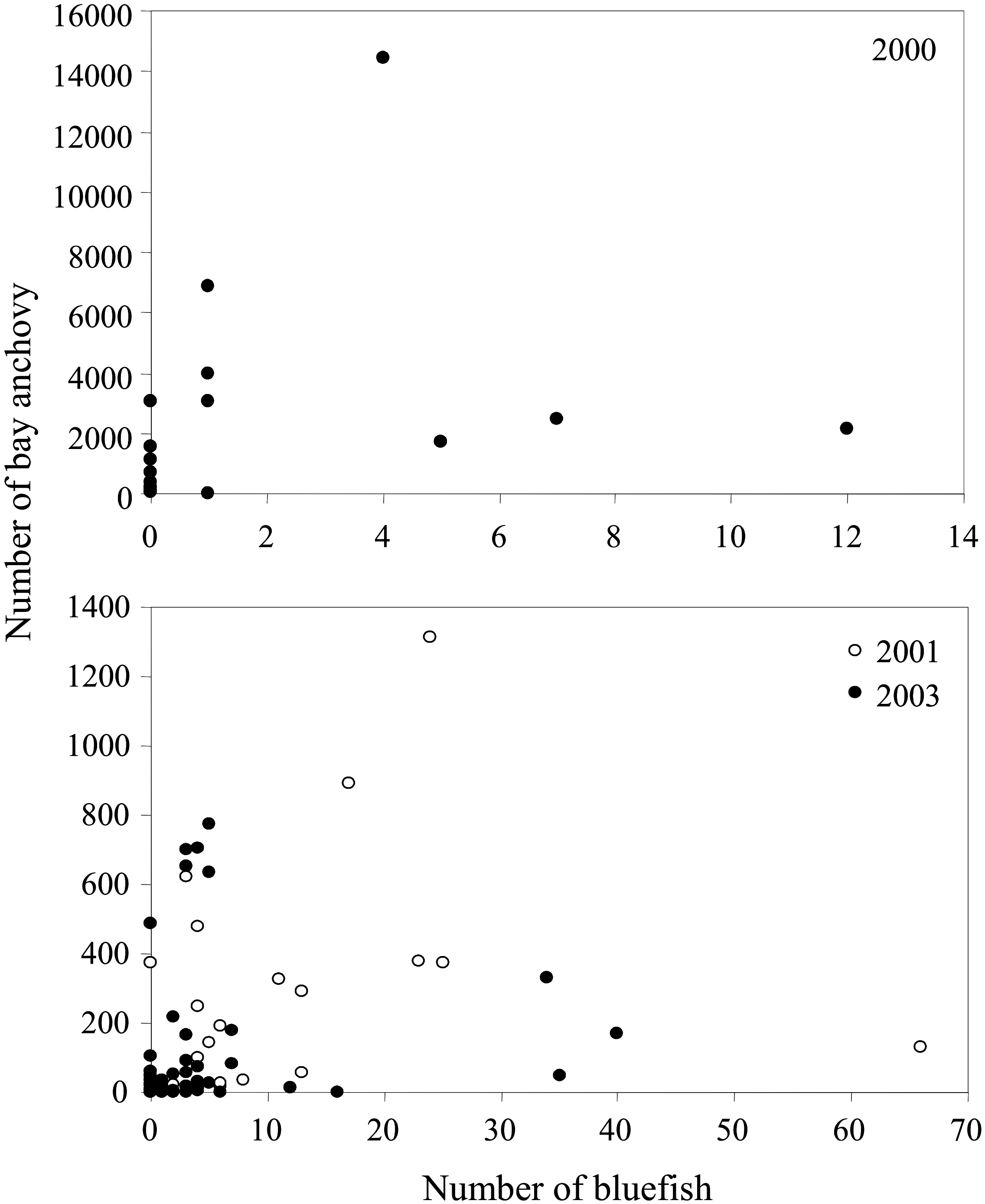


Figure 2.25. Abundance associations of juvenile bluefish and bay anchovy in Maryland coastal waters during 2000 (upper panel) and 2001/2003 (bottom panel). Note difference in x- and y-axis scale between panels. Each data point represents catches during an individual tow (mid-water trawl); data pooled across cruises during which both juvenile bluefish and bay anchovy were present (August and September for 2000, 2001; July – October for 2003.

October) not used in the analyses for the coastal ocean (no sampling in 1999 and different gear type, bottom trawl, in 2004). Mean CPUE of YOY bluefish in these years was 0.50 ± 0.15 SE and 0.26 ± 0.07 SE in 1999 and 2004, respectively; mean annual occurrence was 27% in 1999 and 17% in 2004. Based on mid-water trawl data from all years, mean annual occurrence was significantly different among years (chi-square test of independence, p = 0.0007). Specifically, mean annual occurrence was significantly higher in 1999 v. 2000 (p = 0.0004), 2003 (p = 0.0002), and 2004 (p = 0.0012), but not 2001 (one-way logistic regression, Bonferroni-adjusted (α = 0.005) values for multiple contrasts). Additionally, mean annual occurrence was significantly lower in 2003 than all other years, except 2000 (1999 p = 0.0002, 2001 p = 0.0014, 2004 p = 0.0034).

Bay anchovy relative abundance differed significantly among years in channel habitats of Chesapeake Bay (Kruskal-Wallis test, global p < 0.0001). Specifically, mean annual relative abundance was significantly higher in 2000 than all other years, except 1999 (Fig. 2.23) (p < 0.0001 for 2001, 2003, and 2004: post-hoc nonparametric multiple comparisons with Tukey-adjusted α values). Also, mean annual relative abundance was significantly lower in 2003 than 1999 (p < 0.0001) and 2000 (p < 0.0001).

### *Interannual Comparions, Chesapeake Bay – littoral habitats*

Mean annual occurrence of YOY bluefish differed significantly among years at the Chesapeake Biological Laboratory research pier site (p = 0.003) (Table 2.11). However, sample size in 1999 was low (n = 5 hauls). Tests conducted without 1999 data resulted in a non-significant difference among years (p = 0.36). Generally, bluefish occurrence was higher during the 1999-2001 period (30 – 80% mean annual occurrence) than the 2003 – 2004 period (10 – 20% annual incidence) (Table 2.11). The mean annual

Table 2.11. Interannual and seasonal abundance and occurrence of juvenile bluefish in littoral habitats of Chesapeake Bay. First value in n column refers to the total number of seine hauls conducted in a given year; the number of hauls in early and late season, respectively, are given parenthetically. ‘Early’ season = May – July 31; ‘late’ = August – October. % Occur = the percent of positive hauls for YOY bluefish. Mean CPUE = number of bluefish per seine haul. P-statistic is reported for chi-square tests of differences in incidence of juvenile bluefish among years, between seasons within a year and across years (pooled). Fisher’s Exact test was employed if expected cell frequencies were < 5.

| Annual | | | | Seasonal | | | | |
|---|---|---|---|---|---|---|---|---|
| Year | n | Mean CPUE (± SE) | % Occur (No.) | Mean CPUE (± SE) | | % Occur (No.) | | |
| | | | | Early | Late | Early | Late | p |
| 1999 | 5 (4, 1) | 1.3 ± 1.03 | 80 (4) | 1.4 ± 0.59 | 1 (N/A) | 100 (4) | 0 | 0.2 |
| 2000 | 16 (10, 6) | 0.7 ± 1.31 | 33.3 (6) | 1.2 ± 1.55 | 0 | 60.0 (6) | 0 | 0.03 |
| 2001 | 18 (11, 7) | 0.5 ± 0.99 | 27.8 (3) | 0.7 ± 1.19 | 0.1 ± 0.38 | 36.4 (4) | 14.3 (1) | 0.6 |
| 2003 | 17 (9, 8) | 0.1 ± 0.3 | 10.5 (2) | 0 | 0.3 ± 0.46 | 0 | 25 (2) | 0.2 |
| 2004 | 21 (11, 10) | 0.3 ± 0.56 | 19.2 (5) | 0.6 ± 0.69 | 0 | 45.5 (5) | 0 | 0.03 |
| | | | p = 0.0030 | | | | | |
| Pooled | | | | 0.7 ± 1.1 | 0.1 ± 0.3 | 41.3 (19) | 12.1 (4) | 0.005 |

occurrence of silversides did not differ significantly among years (p = 0.24), and was consistently high across years (75 – 95%) (Table 2.12). Mean annual occurrence of anchovies also did not differ among years (p = 0.11), and was highest in 2000 (47%) and 2004 (30%); lowest in 1999 (0%) and 2003 (12%) (Table 2.13).

Because weekly sampling was conducted at CBL, I was able to statistically test among seasons for this site. Similar seasonal contrasts were not supported in other systems and habitats studied. YOY bluefish were consistently more common during the early season across five years of data (Table 2.11). Data pooled across years indicated that YOY bluefish occurrence was significantly higher during the early season (41% from May – July) than during the late season (12% from August – October) (p = 0.005). Season effects on silverside occurrence were marginally significant using data pooled across years (p = 0.06). In both 2000 and 2004, the occurrence of silversides was significantly higher during the early than the late season (Table 2.12). Also, in these years, mean CPUE was 2 – 3 fold higher during the early than the late season (Table 2.12). Anchovies did not exhibit consistent trends in incidence or relative abundance between early and late seasons (Table 2.13).

### *Seasonal x System Comparisons of Bay Anchovy Abundance*

I compared the relative abundance/occurrence of bay anchovy during June v. later summer and early fall months (July – October composite) in both Maryland coastal waters and mainstem Chesapeake Bay, where sufficient data were available (June data were relatively sparse in each system). The premise of these comparisons was to test whether bay anchovy were more abundant in Chesapeake Bay than the coastal ocean during initial recruitment of the spring cohort to nearshore nursery habitats (see Chapter

Table 2.12. Interannual and seasonal abundance and occurrence of silversides (*Menidia* sp.) in littoral habitats of Chesapeake Bay. First value in n column refers to the total number of seine hauls conducted in a given year; the number of hauls in early and late season, respectively, are given parenthetically. ‘Early’ season = May – July 31; ‘late’ = August – October. % Occur = the percent of positive hauls for YOY bluefish. Mean CPUE = number of silversides per seine haul. P-statistic is reported for chi-square tests for differences in incidence of silversides among years, between seasons within a year and across years (pooled). Fisher’s Exact test was employed if expected cell frequencies were < 5.

| | | Annual | | Seasonal | | | | |
|---|---|---|---|---|---|---|---|---|
| Year | n | Mean CPUE (± SE) | % Occur (No.) | Mean CPUE (± SE) | | % Occur (No.) | | |
| | | | | Early | Late | Early | Late | p |
| 1999 | 5 (4, 1) | 39.2 ± 23.40 | 75.0 (3) | 37.0 ± 28.53 | 50 (N/A) | 75.0 (3) | 100 (1) | 1.0000 |
| 2000 | 16 (10, 6) | 45.3 ± 13.71 | 76.5 (13) | 62.7 ± 19.89 | 20.4 ± 13.91 | 100.0 (10) | 42.9 (3) | 0.0147 |
| 2001 | 18 (11, 7) | 86.8 ± 19.59 | 94.4 (17) | 59.8 ± 22.30 | 129.3 ± 31.64 | 90.9 (10) | 100 (7) | 1.0000 |
| 2003 | 17 (9, 8) | 136.1 ± 79.39 | 94.1 (16) | 37.4 ± 21.10 | 247.0 ± 163.5 | 88.9 (8) | 100 (8) | 1.0000 |
| 2004 | 21 (11, 10) | 19.9 ± 5.80 | 81.0 (17) | 31.9 ± 9.52 | 6.7 ± 3.03 | 100 (11) | 60 (6) | 0.03 |
| | | | p = 0.2423 | | | | | |
| Pooled | | | | | | 91.3 (42) | 75.8 (25) | 0.0576 |

Table 2.13. Interannual and seasonal abundance and occurrence of anchovies (*Anchoa* sp.) in littoral habitats of Chesapeake Bay. First value in n column refers to the total number of seine hauls conducted in a given year; the number of hauls in early and late season, respectively, are given parenthetically. ‘Early’ season = May – July 31; ‘late’ = August – October. % Occur = the percent of positive hauls for YOY bluefish. Mean CPUE = number of silversides per seine haul. P-statistic is reported for chi-square tests for differences in incidence of silversides among years, between seasons within a year and across years (pooled). Fisher’s Exact test was employed if expected cell frequencies were < 5.

| | | Annual | | Seasonal | | | | |
|---|---|---|---|---|---|---|---|---|
| Year | n | Mean CPUE (± SE) | % Occur (No.) | Mean CPUE (± SE) | | % Occur (No.) | | |
| | | | | Early | Late | Early | Late | p |
| 1999 | 5 (4, 1) | 0 | 0 | 0 | 0 | 0 | 0 | |
| 2000 | 16 (10, 6) | 6.4 ± 5.19 | 47.1 (8) | 2.0 ± 3.23 | 12.7 ± 3.87 | 16.7 (2) | 85.7 (6) | 0.0063 |
| 2001 | 18 (11, 7) | 0.7 ± 5.05 | 22.2 (4) | 0 | 1.7 ± 0.55 | 0 | 57.1 (4) | 0.0114 |
| 2003 | 17 (9, 8) | 3.4 ± 5.19 | 11.8 (2) | 6.3 ± 4.53 | 0 | 22.2 (2) | 0 | 0.1558 |
| 2004 | 21 (11, 10) | 11.9 ± 4.67 | 28.6 (6) | 22.7 ± 11.19 | 0 | 54.6 (6) | 0 | .0124 |
| | | | p = .1065 | | | | | |
| Pooled | | | | | | 21.7 (10) | 30.3 (10) | 0.3880 |

1). For June collections, bay anchovy occurrence was consistently higher in Chesapeake Bay (100% across years) than in Maryland coastal waters (19 – 44% across years) (Table 2.14). A series of chi-square analyses were performed using data pooled across years (not shown in Table 2.14). Pooling data across years for each system showed that June incidence was significantly higher in Chesapeake Bay (100%) than in Maryland coastal waters (31%) (chi-square test of independence, $p < 0.0001$). Occurrence during July-October was not significantly different between systems ($p = 0.1$, data pooled across years). In the coastal ocean, occurrence was higher during July – October (65%) than during June (31%) (data pooled across years, $p = 0.0006$), but in Chesapeake Bay, bay anchovy incidence was higher during June (100%) than July – October (73%).

Relative abundance of bay anchovy was significantly lower in the coastal ocean during June than July – October in both 2001 ($p = 0.0006$, Wilcoxon two-sample test) and 2003 ($p = 0.003$). Overall, mean CPUE was an order of magnitude higher in the coastal ocean during summer months v. June (Table 2.14). For the Chesapeake Bay in 1997, no significant difference in bay anchovy abundance occurred between the June and the July – October periods, but abundance was significantly higher during July – October than June in 1999 and 2004 (Table 2.14). In Chesapeake Bay, catches were considerably higher during summer months (~ 400 – 2000 $tow^{-1}$), yet moderate abundances were observed (c. 100 $tow^{-1}$) during June across all years (Table 2.14).

Table 2.14. Comparisons of bay anchovy relative abundance during June v. summer/early fall months (i.e., July – October) in Maryland coastal waters and Chesapeake Bay. Mid-water trawl gear was employed. Mean CPUE = mean number of bay anchovy per tow (± standard error); occurrence reported as percent of positive tows. Wilcoxon two sample tests were employed to test for differences in relative abundance between June and summer/early fall months each year.

**Coastal Ocean**

| Year | Mean CPUE | | Occurrence | |
|---|---|---|---|---|
| | June | July – October | June | July - October |
| 2001 (p = 0.0006) | 44 ± 39.3 | 251 ± 65.7 | 44% (7/16) | 88% (21/24) |
| 2003 (p = 0.003) | 3 ± 2.6 | 122 ± 50.5 | 19% (3/16) | 59% (47/80) |

**Chesapeake Bay**

| Year | Mean CPUE | | Occurrence | |
|---|---|---|---|---|
| | June | July – October | June | July - October |
| 1997 (p = 0.0836) | 734 ± 203.2 | 867 ± 140.4 | 100% (16/16) | 60% (83/138) |
| 1999 (p < 0.0001) | 109 ± 23.2 | 1733 ± 445.8 | 100% (27/27) | 97% (26/27) |
| 2004 (p = 0.0057) | 79 ± 27.1 | 347 ± 56.4 | 100% (12/12) | 98% (47/48) |

## Depth Associations of YOY Bluefish and Bay Anchovy

### *Coastal Ocean*

The occurrence of YOY bluefish was significantly higher in shoal (72%) than deep (35%) waters in the coastal ocean, based on mid-water trawl data pooled across years ($p < 0.0001$, Table 2.15). Furthermore, mean CPUE of bluefish was slightly higher in shoal (9 $tow^{-1}$) v. deep (7 $tow^{-1}$) waters. Bottom trawl data also indicated a significant difference in YOY bluefish relative abundance between depth strata ($p < 0.0004$); mean CPUE was four-fold higher in shoal (100 $tow^{-1}$) than deep (25 $tow^{-1}$) strata.

Bay anchovy relative abundance was also significantly higher in shoal (764 $tow^{-1}$) than deep (351 $tow^{-1}$) waters ($p = 0.0005$), and occurrence was also higher in shoal (80%) v. deep (60%) strata (Table 2.15). No significant differences in mean CPUE of bay anchovy between depth strata were found using bottom trawl data, although mean CPUE was c. 50% higher in shoal v. deep waters (Table 2.15). Striped anchovy relative abundance was significantly higher in shoal (109 $tow^{-1}$) v. deep (14 $tow^{-1}$) waters, based on mid-water trawl data ($p < 0.0001$), and incidence was also higher in shoal (73%) v. deep (50%) strata (Table 2.15). Mean CPUE of striped anchovy was higher in shoal v. deep strata based on bottom trawl data, but the observed difference was not significant for either 10 or 20 minute tow durations (Table 2.15).

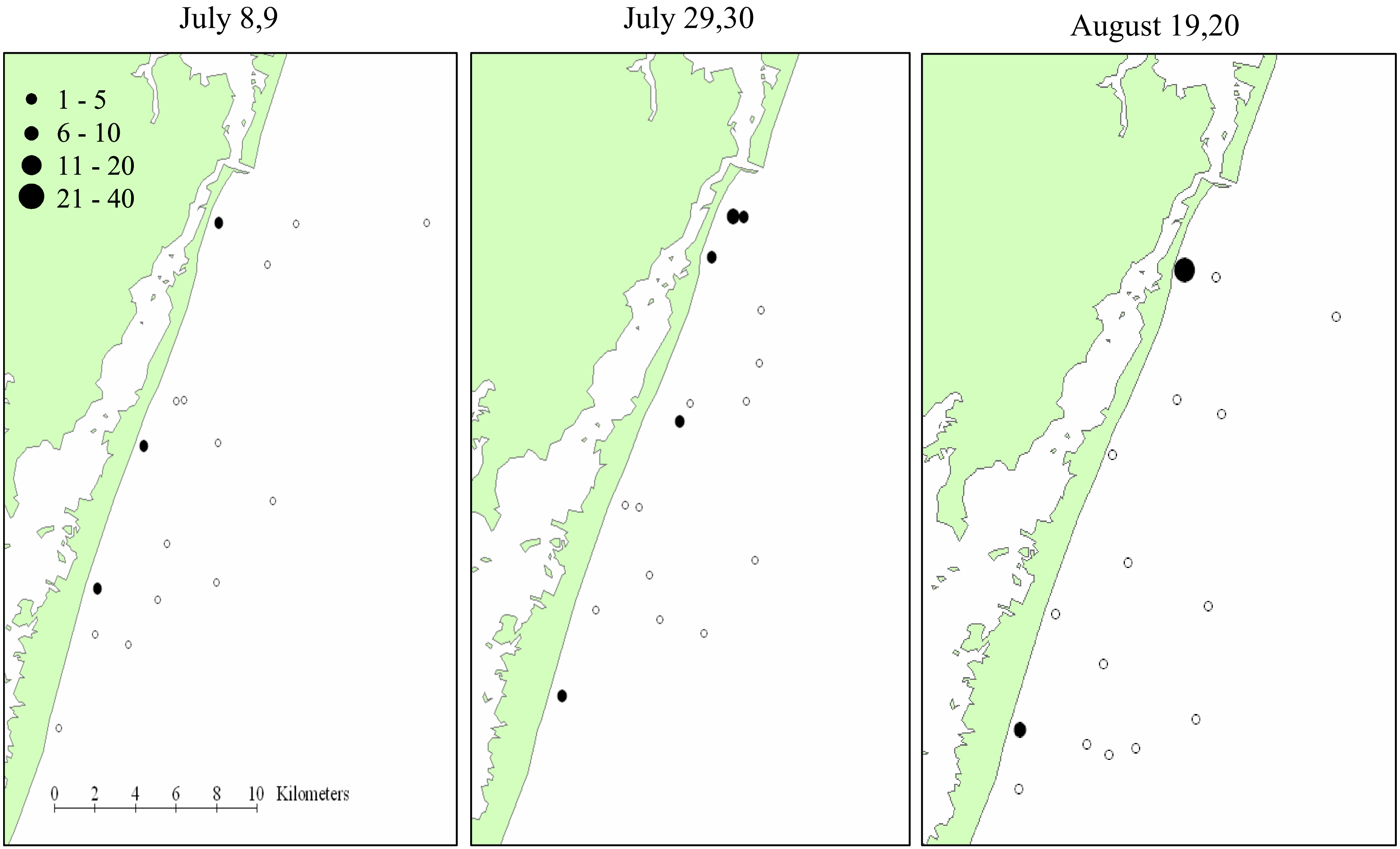
Plots of the spatial distribution of YOY bluefish catches show the general pattern of decreasing abundance with increased distance offshore (i.e., deeper waters) (Figs. 2.26, 2.27). In 2003, YOY bluefish were only present in shoal waters (with the exception of one tow in the inner portion of the “deep” stratum) and at relatively low levels during July – August. During September and October cruises, YOY bluefish were common in

Table 2.15. Comparisons of relative abundance and occurrence of juvenile bluefish, bay anchovy, and striped anchovy between depth strata (shoal ≤ 10 m; deep > 10 m) in Maryland coastal waters and Chesapeake Bay. Both mean catch-per-unit effort (± standard error) and mean percent occurrence (% Occur = the percent of positive tows) reported for a given gear type (MWT = mid-water trawl; B. trawl = bottom trawl). P values for those tests are reported; where no p values are reported (e.g., comparing occurrence of bluefish between strata with bottom trawl data), no tests were conducted. Wilcoxon two-sample tests and chi-square tests of independence were used to test for abundance and occurrence differences, respectively, between depth strata. Note anchovy comparisons utilizing bottom trawl data were restricted to common tow duration. n refers to the number of tows in (shoal, deep) depth strata.

**Coastal Ocean**

| Gear | Mean CPUE (± SE) | | p value | % Occur | | n (s,d) | p value |
|---|---|---|---|---|---|---|---|
| | Shoal | Deep | | Shoal | Deep | | |
| MWT | 9 ± 2.3 | 7 ± 1.6 | | 72 | 35 | 49, 79 | < 0.0001 |
| B. trawl | 104 ± 23.0 | 25 ± 6.6 | 0.0004 | 100 | 81 | 28, 26 | |
| *Bay anchovy* | | | | | | | |
| MWT | 764 ± 238.6 | 351 ± 187.5 | 0.0005 | 80 | 60 | 49, 79 | |
| B. trawl (10 min) | 2108 ± 636.9 | 1242 ± 571.5 | 0.80 | 93 | 73 | 14, 11 | |
| B. trawl (20 min) | 2230 ± 1104.6 | 1721 ± 495.7 | 0.79 | 100 | 82 | 11, 11 | |
| *Striped anchovy* | | | | | | | |
| MWT | 109 ± 46.2 | 14 ± 3.4 | < 0.0001 | 73 | 50 | 49, 79 | |
| B. trawl (10 min) | 452 ± 183.2 | 273 ± 110.3 | 0.45 | 100 | 72 | 14, 11 | |
| B. trawl (20 min) | 7541 ± 5230 | 723 ± 370.2 | 0.43 | 100 | 86 | 6, 7 | |
| **Chesapeake Bay** | | | | | | | |
| *YOY bluefish* | | | | | | | |
| MWT | 0.5 ± 1.1 | 0.2 ± 0.04 | | 19 | 11 | 145, 353 | 0.0141 |
| *Bay anchovy* | | | | | | | |
| MWT | 1180 ± 117.5 | 1548 ± 169.4 | 0.79 | 87 | 80 | 145, 353 | |

Figure 2.26. Spatial distribution of juvenile bluefish catches in Maryland coastal waters during 2003. Mid-water trawl employed for collections; graduated symbols represent catches at individual stations for respective cruises (same graduated scale used across cruises).



July 8,9

July 29,30

August 19,20

Figure 2.26. continued

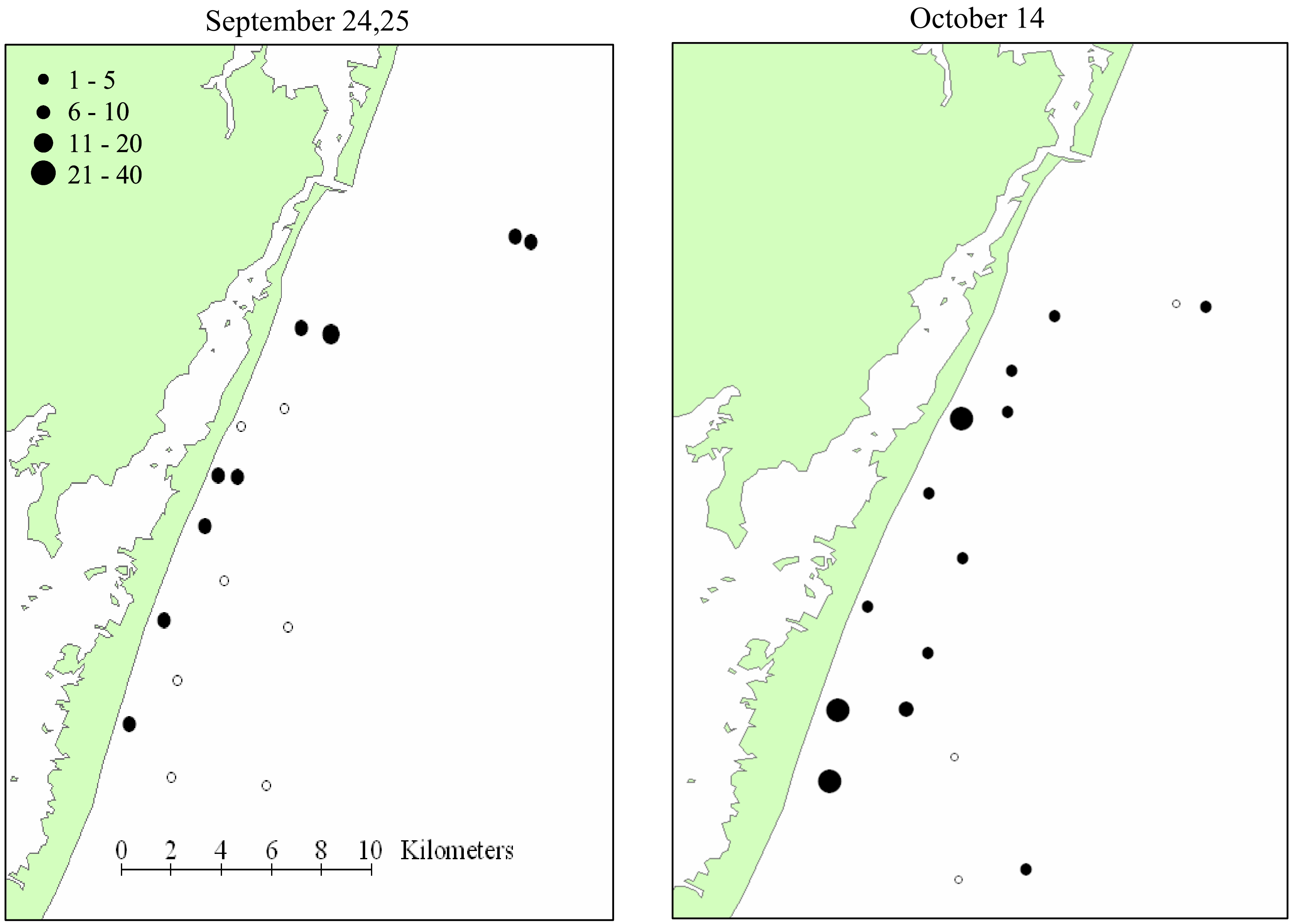


Figure 2.27. Spatial distribution of juvenile bluefish catches in Maryland coastal waters during 2004. Mid-water trawl employed for collections; catches are standardized to number per 20 minute tow. Graduated symbols represent catches at individual stations for respective cruises (same graduated scale used across cruises).

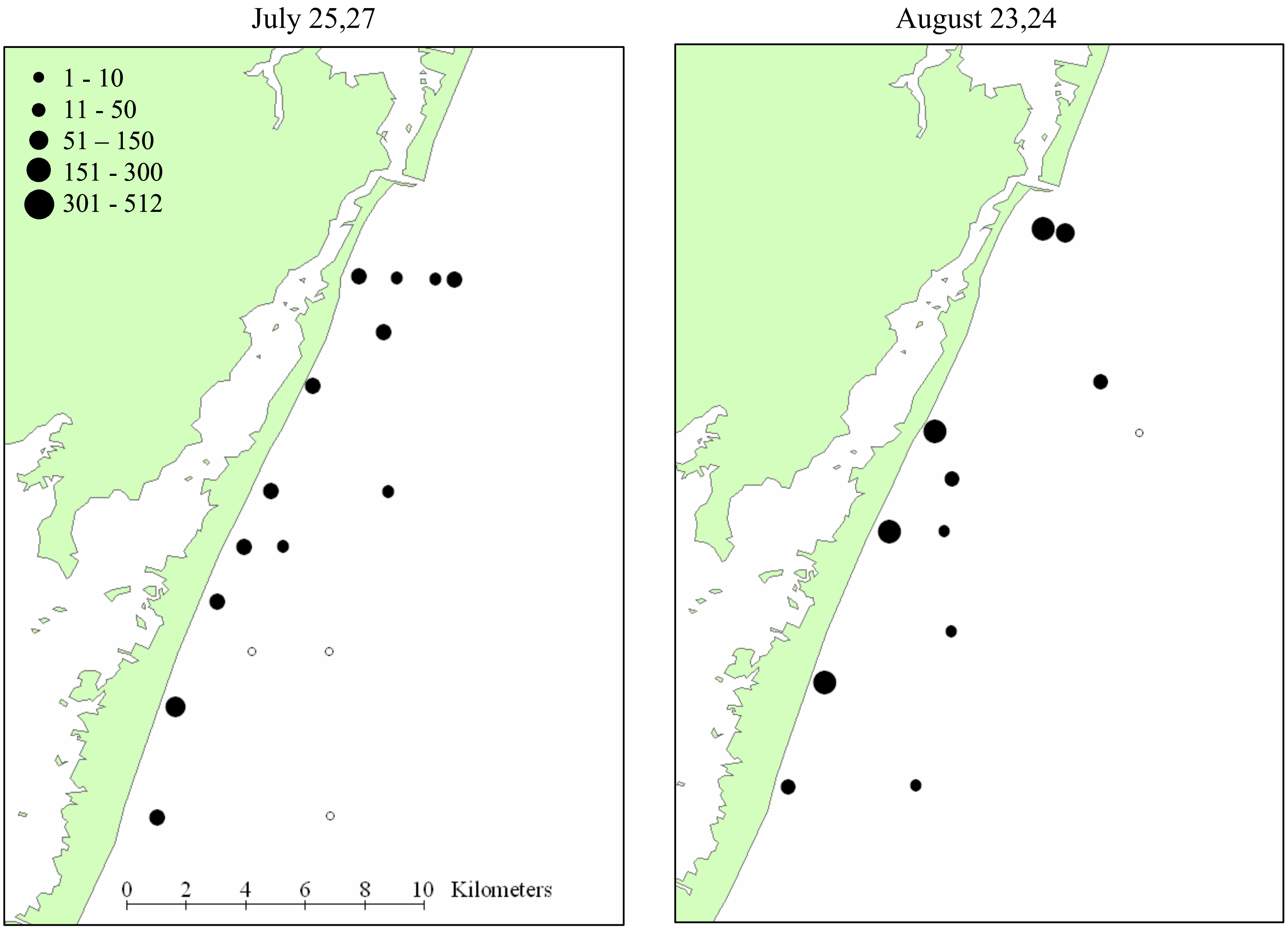
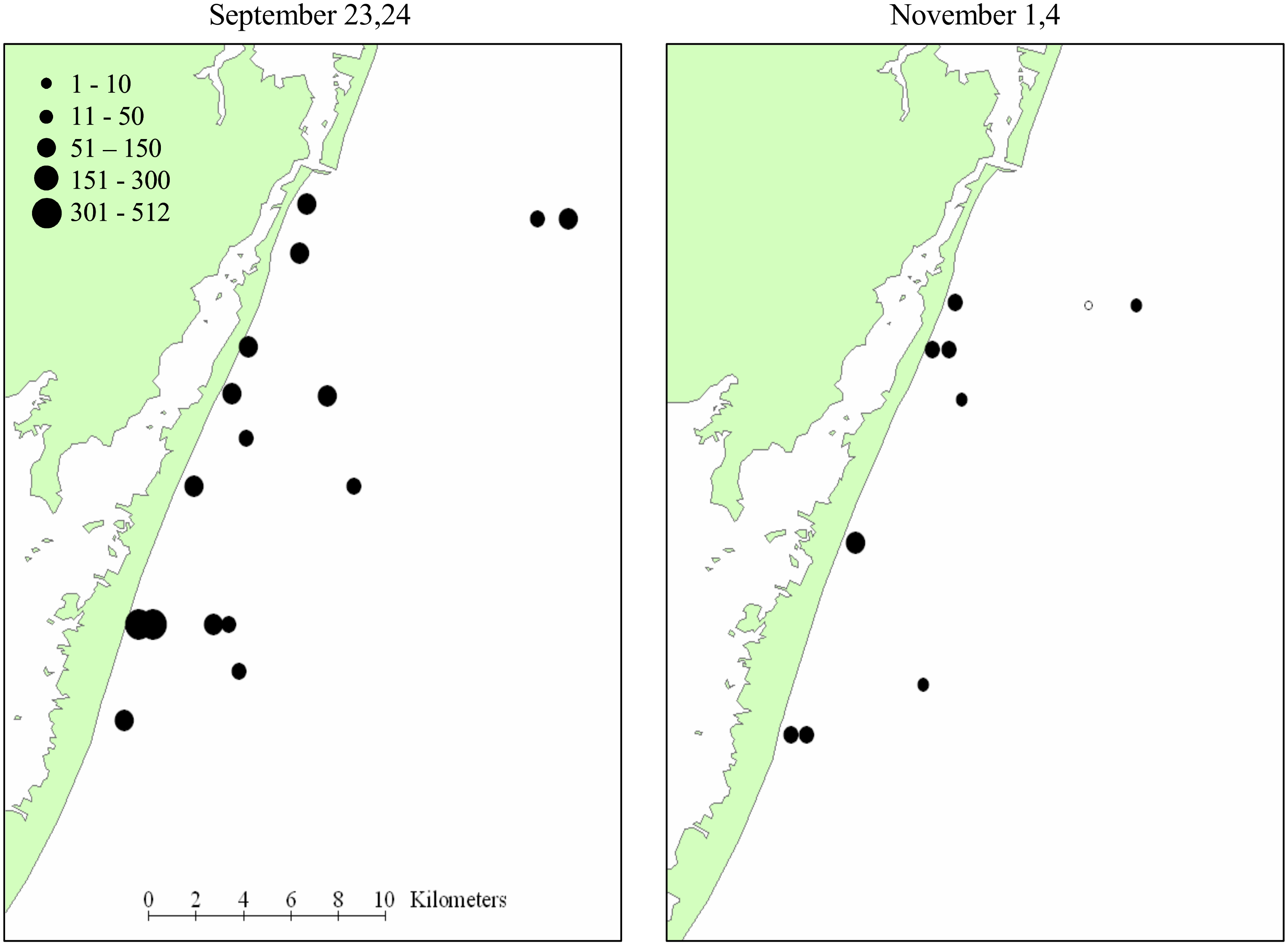


Figure 2.27. continued

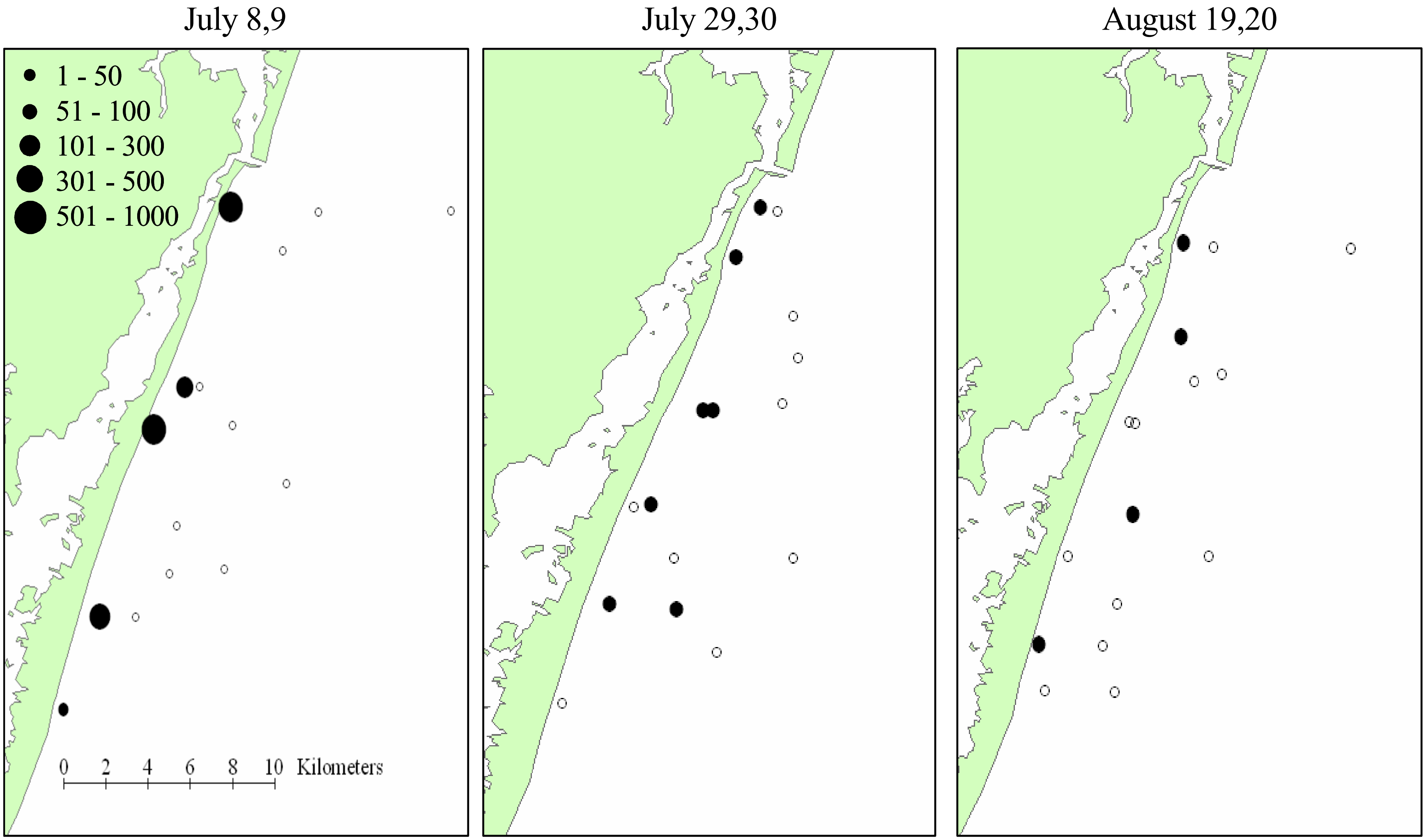


both deeper offshore waters (1 – 6 km from shore, 9 – 18 m depth) and shoal regions, but catches remained highest in shoal waters (Fig. 2.26). Spatial distributions of bay anchovy catches in 2003 were similar to those for YOY bluefish: limited to shoal waters in July and August and common in both shoal and deeper offshore waters during September and October (Fig. 2.28). In 2004, YOY bluefish were common in both deeper offshore and shoal waters across cruises (Fig. 2.27). However, catches were considerably higher in shoal habitats, especially during August and September. Bay anchovy catches in 2004 were not consistently higher in shoal or deep waters, except during August, when they were concentrated in shoal regions (Fig. 2.29).

*Chesapeake Bay*

YOY bluefish occurrence was significantly higher in shoal (19%) than deep (11%) waters of Chesapeake Bay, based on mid-water trawl data pooled across five years ($p = 0.01$) (Table 2.15). Also, mean CPUE of YOY bluefish was marginally higher in shoal (0.5 $\text{tow}^{-1}$) v. deep (0.2 $\text{tow}^{-1}$) regions (Table 2.15). Bay anchovy relative abundance was not significantly different between depth zones in Chesapeake Bay, based on pooled mid-water trawl data.

Figure 2.28. Spatial distribution of bay anchovy catches in Maryland coastal waters during 2003. Mid-water trawl employed for collections; graduated symbols represent catches at individual stations for respective cruises (same graduated scale used across cruises).

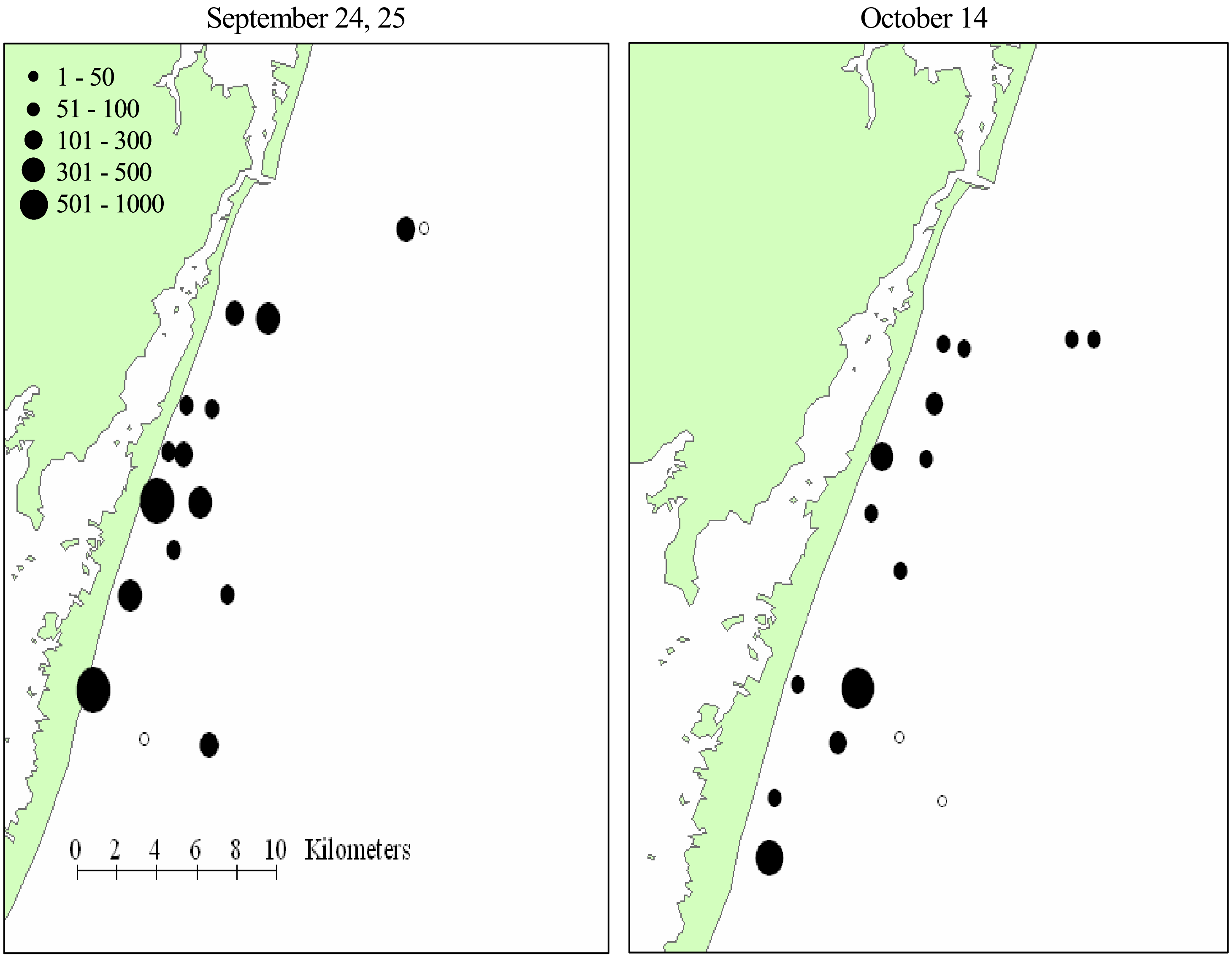


July 8,9

July 29,30

August 19,20

Figure 2.28 continued



September 24, 25

October 14

Figure 2.29. Spatial distribution of bay anchovy catches in Maryland coastal waters during 2004. Bottom trawl employed for collections. Because no significant differences existed in catches between ten and twenty minute tow durations, reported catches are pooled over tow durations for a given cruise. Graduated symbols represent catches at individual stations for respective cruises (same graduated scale used across cruises).

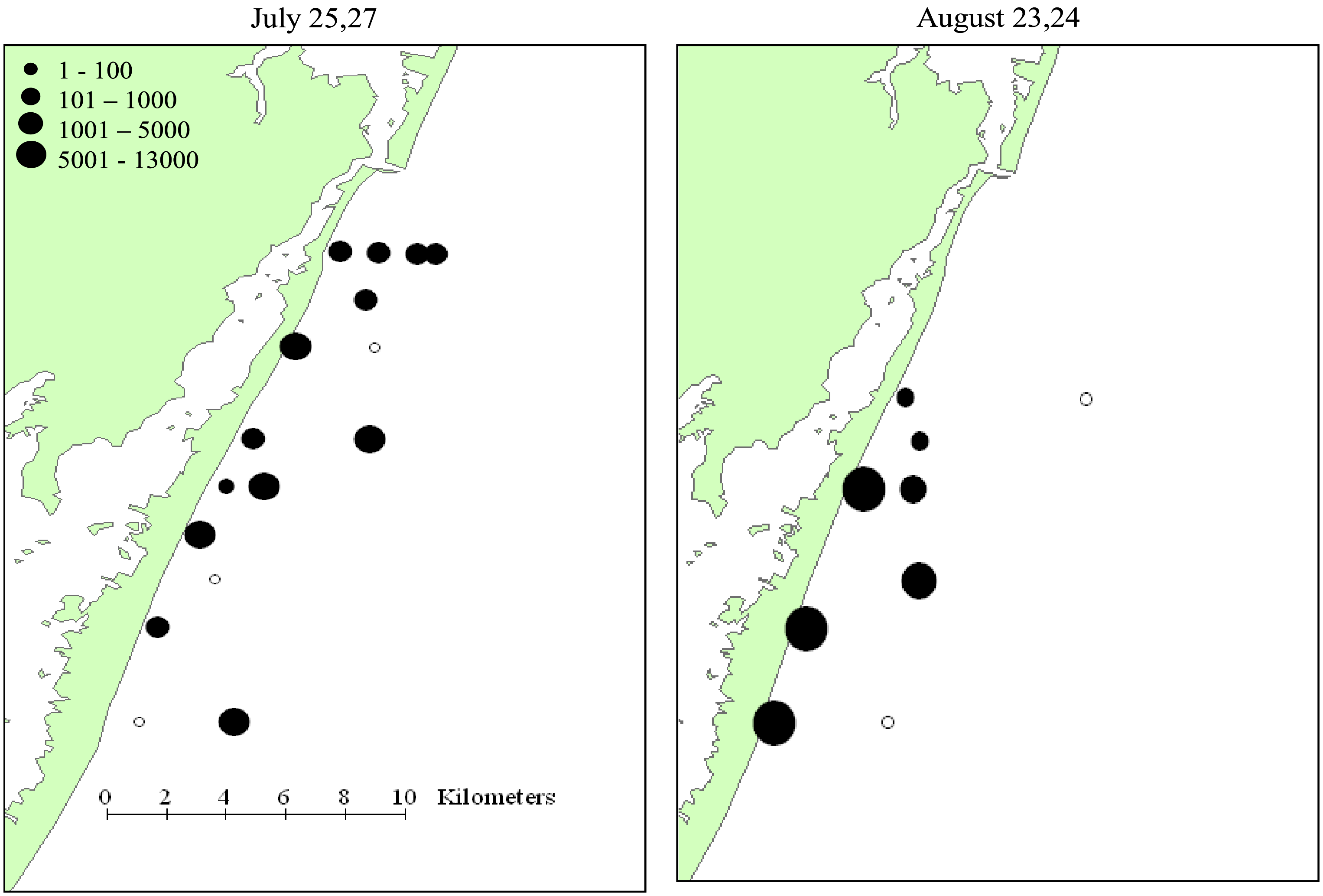
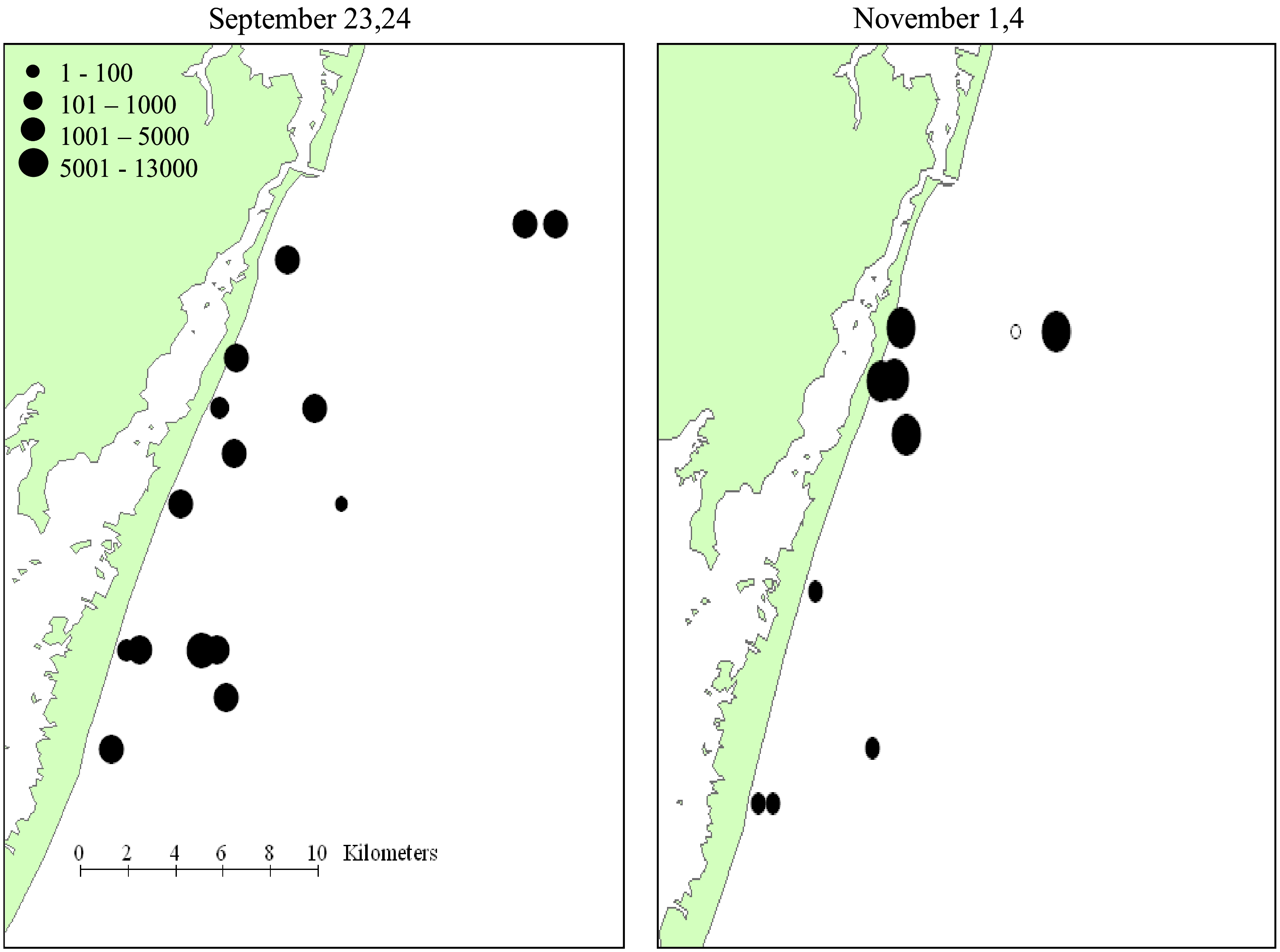


Figure 2.29. continued


September 23,24

November 1,4

## Discussion

This study demonstrated that coastal ocean habitats function as important feeding grounds for young-of-the-year juvenile bluefish. Juveniles were chiefly piscivorous across systems and habitats, although invertebrate prey was moderately important for juveniles inhabiting coastal ocean environments. Bay anchovy dominated diets in the coastal ocean and channel habitats of Chesapeake Bay, whereas silversides (*Menidia* sp.) dominated diets in littoral habitats of Chesapeake Bay. Significant interannual differences in diet composition were found in both coastal ocean and estuarine habitats, and significant seasonal differences occurred in Chesapeake Bay. Juvenile bluefish were almost completely piscivorous by 80 mm TL and consistently selected small bay anchovy in the coastal ocean.

Within the coastal ocean, juvenile bluefish and their principal prey, bay anchovy, exhibited significantly higher abundances in shoal (< 10 m) v. deep (10 – 18 m) waters, supporting my hypothesis of a positive association of juvenile bluefish and bay anchovy abundances. Further, occurrence of juvenile bluefish was significantly higher across years in Maryland coastal waters than Chesapeake Bay, supporting my hypothesis that juvenile bluefish are not strictly estuarine dependent. Finally, the relative abundance of bay anchovy was significantly higher in mainstem Chesapeake Bay than Maryland coastal waters, yet abundances were still fairly high (median catches of 500 – 1,000 $\text{tow}^{-1}$) in the coastal ocean.

### *Diet Trends in Maryland Coastal Waters*

The most prominent difference in diet composition of YOY bluefish from the coastal ocean was due to interannual effects. The incidence of anchovy prey was significantly lower in 2003 than in 2001 or 2000. Interestingly, annual feeding incidence on anchovies was positively associated with annual relative abundance patterns of bay anchovy. Both the incidence of anchovy as prey and their relative environmental abundance were significantly lower in 2003 v. 2000 and 2001 (Figs. 2.4, 2.23).

Diet composition of bluefish from 2004 bottom trawl samples was similar (anchovies dominant with only moderate invertebrate contributions) to that in 2000 and 2001 mid-water trawl collections, but biases between gear types could preclude inferences on similarity among years. For instance, one might expect piscine prey (i.e., anchovy) to be more common for YOY bluefish collected with a large bottom trawl (2004) than a small mid-water trawl (2000 – 01; 03) due to its increased fishing power and associated increased likelihood of net feeding. Although the incidence of net feeding was slightly higher for bottom trawl (2004) than mid-water trawl (2003) collections, differences between years were not significant on a per-tow basis (10% and 20% for mid-water and bottom trawl, respectively, $p = 0.09$) or a per-fish basis (10% or 6%, for mid-water and bottom trawl, respectively, $p = 0.17$). Moreover, diet data in 2003 and 2004 was screened for net feeding (see Methods), thus mitigating any potential biases between or within gear types. Net feeding was not assessed for 2000 and 2001 samples, hence, the contribution of anchovy may have been slightly over-estimated. The incidence of unidentified fish prey was rather high in 2000 and moderate in 2001. Yet, assuming most unidentified fish prey represented *Anchoa sp*., this would result in even higher similarity (i.e., anchovies nearly 100% FO) among 2000, 2001, and 2004 diets. Indeed, on a per tow basis, incidence of anchovy prey was 90 – 100% across 2000, 2001, and 2004, but only 60% in 2003. Therefore, because gear types and analytical (laboratory) procedures did not appear to bias diet composition indices across years; incorporating 2004 diet results (also the year when most diets were analyzed, n = 451) further supports my interpretations of a diet difference in 2003.

Interannual differences in the degree of invertebrate foraging by YOY bluefish has been noted elsewhere. Buckel et al. (1999a) reported a complete absence of invertebrates in guts of summer-spawned YOY bluefish collected in Middle Atlantic coastal waters in 1995; whereas in 1994, fish prey (bay anchovy) showed only a ~50% FO and invertebrates (particularly mysids) were common (~20% FO). Friedland et al. (1988) observed that invertebrates (sand, mysid, and grass shrimps) dominated diets (60-80% FO) in two of three years for YOY samples collected in Sandy Hook Bay, NJ; fish (mainly silversides) dominated diets in the other year (66.3% FO).

Few seasonal differences in diet were observed in the coastal ocean (Fig. 2.5). Interestingly, the only evidence of cannibalism (n=4, or 1.4% FO) occurred during August of 2004, when initial recruitment of small members of the summer cohort was observed (see Chapter 1). The largest size disparity between spring- and summer-spawned bluefish occurred during August and one might expect cannibalism to occur at this time. Buckel et al. (1999a) also reported low levels of cannibalism by the spring cohort on the summer cohort (September – October) in the coastal ocean, 1.1 – 1.9% FO, across years.

### Diet Trends in Chesapeake Bay

Seasonal and interannual differences in diet composition for juvenile bluefish collected in littoral habitats of Chesapeake Bay were associated with abundance patterns of prey. Silversides typically dominated diets, except in 2004, when there was lower feeding incidence on silversides (Fig. 2.9). In 2004, other fish prey (anchovies and clupeids) occurred at much higher incidence and importance levels. In the Patuxent River, relative abundance of silversides was lowest, and anchovies highest, in 2004 compared to other years (Tables 2.12, 2.13). However, relative abundance trends at this one site were not likely representative of bay-wide (Maryland portion) patterns. Indeed, the Maryland DNR seine survey (which samples all major sub-estuaries) indicated similar abundances of silverside in 1999 and 2001 (11 – 12 geometric mean per haul (g.h.)), which were two-fold higher than in 2000, 2003, and 2004 (g.h. ~ 5 across years). Hence, we cannot generalize results from the Patuxent River site to the Chesapeake Bay. Moronid prey were present in stomachs from 1999-2001, but absent in 2003 and 2004. This was consistent with striped bass juvenile abundance trends in the MD DNR seine survey: 5-13 g.h. in 1999-2001, and 4 g.h. in 2004 (2003 not considered because of low diet sample size).

Silversides occurred as prey items at higher incidence earlier in the season for YOY feeding in littoral habitats (Figs. 2.9, 2.16; Table 2.12). YOY bluefish also consumed silverside prey during the late season, although anchovies became the more common prey during this period. Although not significantly more common, the incidence of moronid and clupeid prey was also higher in the early season. The higher incidences and importance of silverside, moronid, and clupeid prey during early summer in littoral estuarine habitats is likely related to spring spawning peaks and resultant availability of these species as prey at small juvenile sizes for spring-cohort YOY bluefish.

Other studies have reported similar seasonal shift in diets of YOY bluefish collected in estuaries. Juanes and Conover (1995) found that silversides dominated diets (40 – 50% FO; 45 – 70 % W across two years) of spring-spawned bluefish in early summer in Great South Bay, with grass/sand shrimp also common (10 – 35% FO); whereas similar-sized (90 – 120 mm) summer-spawned YOY collected in late August and through September relied almost exclusively on bay anchovy (45 – 86% FO; 65 – 84% W). Additionally, Buckel et al. (1999b) reported both interannual and seasonal variations in diets for YOY bluefish collected in the Hudson River from 1990-1993. Striped bass dominated diets in two of four years (40 – 60 %W), and either silversides (50% W) or bay anchovy (60% W) were most important in the two other years. Further, striped bass prey were nearly absent from diets in 1991, when its lowest relative abundances were observed. In regards to seasonal differences, Buckel et al. (1999b) found striped bass generally dominated diets of YOY collected in June and July and bay anchovy typically dominated diets of summer-spawned bluefish collected from August – October across all four years.

While moronids, particularly juvenile striped bass, *Morone saxatilis*, appear to be an important component of spring-spawned bluefish diets in the Hudson River, they were of minimal importance and not common in diets in other estuarine systems. In the Hudson River: Buckel et al. (1999b) found that striped bass comprised c. 40% of diets by weight across four years (except 1991, see above), and Juanes et al. (1993) reported 5 –

20% FO and 8 – 17% W in 1989. In Chesapeake Bay, I observed lower contributions of moronids: 2 – 6% for both FO and W across 1999-2001, and an absence of moronids in diets in 2004. Moronids could not be identified to species level in this study. Some moronid prey were likely white perch *Morone americana*; thus, my diet values may represent an overestimate of striped bass in the diets of YOY bluefish. Other diet studies in MAB estuaries noted a complete absence of moronids from YOY bluefish diets: Great South Bay, NY (Juanes et al. 1994); Piankatank River, VA (Harding and Mann 2001); Sandy Hook Bay, NJ (Friedland et al. 1998; Scharf et al. 2004).

Diet studies focused in the Hudson River system concluded that juvenile bluefish exert top-down control on juvenile striped bass, resulting in substantial mortality and negatively impacting recruitment of this economically and recreationally important species (Juanes et al. 1993; Buckel et al. 1999b, Buckel and Stoner 2000). However, in other MAB estuaries throughout the range of the striped bass population, striped bass do not seem to be an important component of diets. Accordingly, on a population-wide scale, bluefish predation on striped bass may not represent a significant source of mortality. The high reliance of YOY bluefish on moronids in the Hudson River may be anomalous. Interestingly, Boreman and Goodyear (1988) found evidence of substantial mortality (35 – 79% of the standing stock) of YOY anchovy associated with power plant entrainment in the Hudson River. Buckel et al. (1999b) suggested this may lead to decreased availability of anchovy, and in turn YOY bluefish may resort to foraging on YOY striped bass.

Within Chesapeake Bay, principal prey differed for YOY bluefish collected in littoral (< 1.5 m depth) v. open-water (4 – 40 m depth) habitats. Anchovies dominated the diets of bluefish collected by mid-water trawl in mainstem regions of Chesapeake Bay, whereas silversides were the most important prey item of juveniles collected in littoral habitats with a beach seine. Silverside prey were present, but rare (0 – 9% FO), for YOY bluefish collected in mainstem regions. Silversides are a schooling species which are very common in shore zones of estuaries and their tributaries. In contrast, bay anchovy are ubiquitously distributed in estuaries, but may prefer open-water habitats. Hartman and Brandt (1995a) also found that bay anchovy dominated the diets (60 – 100 %W) of YOY bluefish collected in channel regions of Chesapeake Bay from May – October in 1990 and 1991.

Littoral habitats in Chesapeake Bay may be more important foraging areas than mainstem, channel habitats. Mainstem regions may primarily serve as a "migratory corridor", while littoral habitats may afford more suitable "resident" habitats. The availability of small, piscine prey is likely higher, and predation risk lower (fewer large predators), in littoral v. channel habitats. Accordingly, mainstem regions would be critical foraging regions (with high abundances of bay anchovy) for migrating YOY bluefish during late spring and early fall, with littoral habitats providing foraging grounds (mainly silversides) throughout the entire summer growing season. While the intensity of mid-water trawl sampling in mainstem regions of Chesapeake Bay was high, the temporal frequency was too low (only two major cruises: generally July and October) to confidently estimate seasonal patterns of abundance of juvenile bluefish within channel habitats of Chesapeake Bay to examine the possibility that YOY bluefish may chiefly utilize mainstem regions as "migratory corridors." Interestingly though, from a qualitative (different gear types) standpoint, mean annual relative abundance (CPUE) of

YOY bluefish was consistently higher in littoral (0.3 – 1.3 per seine haul) v. channel (0.1 – 0.5 per mid-water tow) habitats across years 1999, 2000, 2001, and 2004 (2003 not included because of low sample size).

Despite the fact that all YOY bluefish samples from mainstem regions were collected at night, feeding incidence was still fairly high (70 – 84%) and similar to values for littoral habitats (73 – 86% across years), for which all collections were made in daylight. Feeding incidence was only 30% for the 2004 sample from mainstem Chesapeake Bay, but this value may be a consequence of small bluefish sizes (30 – 50 mm) and low sample size (n = 17). The relatively high nocturnal feeding incidence for bluefish has not been previously observed, although Buckel and Conover (1997) suggested that increased feeding could occur during full moons. Previous studies have found gut fullness values of YOY bluefish generally peak at dawn and crepuscular periods, remain high throughout the day and decline to low values at night (Juanes and Conover 1994b, Buckel and Conover 1997, Buckel et al. 1999).

In estuaries, juvenile fish diets can be influenced by microhabitat characteristics associated with bottom type or water quality, which could not be examined in my study due to the low occurrence of YOY bluefish in MD DNR collections. These features may be important for YOY bluefish. For instance, Harding and Mann (2001) concluded that diversity of piscine prey was higher for YOY bluefish collected at oyster reef v. sandy bottom habitats in the Piankatank River, a sub-estuary in the Virginia portion of Chesapeake Bay.

### *Diet patterns between systems*

Invertebrate prey was more common and important for juvenile bluefish inhabiting the coastal ocean than Chesapeake Bay. In littoral habitats of Chesapeake Bay, YOY bluefish consumed invertebrates (6 – 20% FO among years), but very high feeding incidence on fish prey (96%) indicated that piscivory was a more dominant mode. In the coastal ocean, invertebrate prey was common, especially in 2003 (54% FO) and 2001 (29% FO). Moreover, 25% and 11% of bluefish stomachs in 2003 and 2001, respectively, contained only invertebrate prey. Hence, some juvenile bluefish in the coastal ocean appeared to rely exclusively on invertebrate prey. Invertebrate prey was also common (61% FO) in littoral surf-zone habitats along Maryland's barrier islands.

Mysid shrimp were the most common and important invertebrate prey in the coastal ocean across years. Other invertebrate prey types were diverse, but uncommon (Table 2.4), except in 2003 when crab megalopae, sand shrimp, and calanoid copepods were fairly common. Mysids were a common prey (34% FO) for YOY bluefish collected in sandy-bottom surf zone habitats (Table 2.5). In contrast to coastal environments, mysids were virtually absent in diets of Chesapeake Bay YOY; polychaetes were the most common invertebrate prey (especially in littoral habitats). Hartman and Brandt (1995) noted that mysids were a common prey type for YOY weakfish collected in Delaware Bay, but were absent in guts from mainstem Chesapeake Bay collections, and suggested that hypoxia limited the occurrence and abundance of mysids in Chesapeake Bay during summer. Interestingly, Buckel et al. (1999a) observed, among all sampled regions of the MAB shelf, the highest incidences of mysid shrimp prey (12% FO) for YOY bluefish collected in the "Chesapeake-Delaware" region, the region most proximate to the sampling domain in this study. The presence of refractory miscellaneous items such as wood, sand grains, macroalgae, grass blades, etc. was more common in 2003 (15%) than in 2004 (2%) samples. Incidence of benthic debris may be associated with incidental ingestion when feeding on benthic invertebrates (e.g., sand shrimp, mysids) and was consistent with the higher contribution of invertebrate prey in 2003. YOY bluefish in the coastal ocean also consumed pelagic invertebrate prey in 2003, namely crab megalopae and calanoid copepods. Crab megalopae were also a common prey type (28% FO) for YOY bluefish collected in the surf-zone across years. Finally, the occurrence (7 – 22% FO) and importance (0 – 7 %W) of invertebrate prey I observed in Chesapeake Bay littoral habitats were substantially less than reported in other MAB estuaries: Great South Bay, NY (sand and grass shrimp, 22-39% FO and 22-50% W; Juanes and Conover 1994a), Sandy Hook Bay, NJ (56-72% FO, 31-46 % W; Friedland et al. 1988), and Marsh River, ME (sand shrimp, 40-70% FO and 23-40% W; Creaser and Perkins 1994).

Although types of invertebrates may differ between estuarine and coastal environments (due to substrate differences, differing communities among microhabitats, etc.), abundances of invertebrates are probably high in both systems, suggesting that YOY bluefish may select piscine prey over invertebrate prey. YOY bluefish are capable of nearly complete piscivory upon arrival to nursery habitats (Fig. 2.18; Marks and Conover 1993) and growth rates are higher on a fish- than invertebrate-based diet (Juanes and Conover 1994a). Therefore, chiefly piscivorous feeding habits should maximize growth of young bluefish. Meanwhile, relatively high consumption of invertebrates in a particular habitat or time period might suggest suboptimal foraging conditions.

Accordingly, habitats with a higher diversity of potential piscine prey could be important in sustaining bluefish production. Higher diversity of piscine prey would provide a buffer against environmental conditions that might select against production of a single prey species in a given year.

The diversity of piscine prey was greater for juvenile bluefish collected in Chesapeake Bay than Maryland coastal waters. In the coastal ocean, *Anchoa sp.* alone (mainly bay anchovy) dominated diets, with other piscine prey contributing < 4% FO across years. Interestingly, in 2003, low incidence of feeding on anchovy in the coastal ocean did not correspond with substitution of piscine prey (e.g., butterfish, clupeids, sciaenids), but rather an increased reliance on invertebrate prey (mysids, sand shrimp, and crab megalopae) and fish larvae. A similar pattern emerged in 2001 (Table 2.4). These results indicate that suitable alternative piscine prey in coastal ocean environments may be rather low or less available to YOY bluefish than in the Chesapeake Bay and other estuaries.

Striped anchovy represents one possible of source of diet diversity for coastal YOY bluefish. The incidence of striped anchovy in diets was considerably higher in 2003 (40%) than 2004 (15%), which was converse to the pattern of bay anchovy in diets (Table 2.4). The larger size of striped anchovy may serve as a refuge from predation. The mean total lengths of striped anchovy typically exceeded 100 mm and predator-prey total length ratios were ~0.7 (Table 2.9). The average size of YOY bluefish that consumed striped anchovy was 140 mm (n = 10) in 2003 and 170 mm (n = 4) in 2004. Thus, striped anchovy may be more important prey for larger spring-spawned bluefish or age 1+ bluefish in the coastal ocean. Buckel et al. (1999a) found that striped anchovy were relatively common (1 – 13% FO) and important (2 – 33% W) prey for spring-spawned bluefish (161 – 300 mm fork length across years) collected in MAB shelf waters during September, while striped anchovy prey were absent in stomachs of summer-spawned bluefish (37 – 160 mm FL) across years. Striped anchovy could be an important prey item during specific times following peaks in spawning activity, because small striped anchovy potentially would be available to YOY bluefish. But, little is known about the spatiotemporal aspects of reproduction of striped anchovy (Able and Fahay 1998). Sciaenids (e.g., weakfish) are extremely abundant in Maryland coastal waters, however most individuals in our trawl samples appeared to be yearlings (> 120 mm TL) and probably are not important substitute piscine prey in coastal ocean environments, although they may be important for yearling bluefish.

The higher diversity of piscine prey observed for juvenile bluefish collected in Chesapeake Bay (namely littoral habitats) v. Maryland coastal waters is likely due to the high diversity of small juvenile fishes typically found in estuarine habitats. For instance, I observed moderate incidence levels of moronid and clupeid prey for YOY bluefish (Table 2.6); juveniles from these families (e.g., anadromous species such as striped bass *Morone saxatilis*, white perch *Morone americana*, and various *Alosa sp.*) rely on estuaries as nursery grounds. Interestingly in 2004, when low incidence of otherwise dominant silverside prey was observed, YOY bluefish appeared to switch to consumption of other piscine prey types (anchovies and clupeids). In contrast, when incidence of principal prey (anchovies) was low in the coastal ocean during 2003, YOY bluefish switched to consumption of invertebrates, suggesting again a lack of availability of piscine species other than anchovy as prey in coastal ocean environments.

### *Depth (Spatial) Associations of YOY Bluefish and Bay Anchovy in the Coastal Ocean*

Shallow waters of coastal ocean environments, just outside the surf zone to 10 m depth (< 1 km from shore), function as important foraging areas for juvenile bluefish. My results demonstrate that occurrence and abundances of YOY bluefish were positively associated with their principal prey, bay anchovy, in the coastal ocean, both more abundant in shoal (< 10 m) than deep (10 – 18 m) waters (Table 2.15). Spatial distribution plots (Figs. 2.26 – 2.29) also revealed that catches of both YOY bluefish and bay anchovy were higher in shoal v. deep waters.

Bay anchovy relative abundances were significantly higher in shoal v. deep waters based on mid-water trawl data, and although 50% higher in shoal bottom trawl samples, the difference with deep waters was not significant. Anchovy catch data based on our bottom trawl collections (2004 only) may be less reliable than mid-water trawl samples. Wing and belly mesh of the bottom trawl were substantially larger than for the mid-water trawl, which probably results in a lower selectivity for anchovy. As evidence, differences in tow duration (10 v. 20 minutes) resulted in no consistent difference between anchovy catches (although catches were highly variable).

Despite evidence for increased availability of anchovies in shoal coastal waters, incidences of anchovy prey were similar between strata (Fig. 2.6). Encounter probabilities, based on density, should be higher in shoal v. deep waters; indeed, highest abundances of YOY anchovy occurred in shoal waters, which likely serve as important foraging arenas for YOY bluefish. However, my results also show that feeding occurs in deeper waters. Perhaps encounter probabilities are similar in deeper waters because anchovy densities are still moderate (Figs. 2.28, 2.29) and there exists improved maneuverability and fields of vision by YOY bluefish in deeper water. Also, feeding frenzies may be common in shoal waters due to high densities of both YOY bluefish and bay anchovy, and agonistic feeding behaviors (e.g., prey stealing) associated with feeding in schools (Juanes and Conover 1994b) could reduce effectiveness of foraging in these shoal areas. Finally, invertebrates are the primary alternative prey when anchovy are less abundant (see above); in 2003 when invertebrates were common in diets, their incidence as prey was higher in deep v. shoal waters, suggesting that invertebrates may be important in regions (deep waters) where anchovy abundance is lower.

Other studies have demonstrated that juvenile bluefish abundance is much higher in shoal than deep waters within the coastal ocean. Able et al. (2003) observed the relative abundance of YOY bluefish was consistently $\geq$ 2-fold higher in shallow (5 – 10 m depth) than deep (11 – 30 m) waters across four years of bottom trawl collections in coastal ocean environments off New Jersey. Further, Able et al. (2003) found that, in one year, YOY bluefish were only present in shoal waters. Munch (1997) reported that the highest abundances of spring- and summer-spawned bluefish occurred in depths of 5 – 15 m and 5 – 10 m, respectively, based on 23 years of data from the National Marine Fisheries Service (NMFS) fall bottom trawl survey. The fact that juvenile bluefish abundance is particularly high in shoal habitats of the coastal ocean has important management implications for this species. Data from the NMFS fall bottom trawl survey is currently used as the index of YOY recruitment of bluefish, which is utilized in stock assessments. Bottom trawl tows for this survey occur in relatively deep waters of the MAB shelf. A recent 2004 cruise report indicated that depths < 18 m were not sampled.

Given that YOY bluefish abundance is substantially higher in shoal (5 – 10 m) depths within the coastal ocean (this study; Munch 1997; Able et al. 2003); recruitment indices based on NMFS trawl data may underestimate the abundance of YOY bluefish, especially the contribution of summer-spawned individuals, which may primarily utilize shoal coastal ocean nursery grounds (Chapter 1). The timing of emigration of YOY bluefish from estuaries could also influence/bias this index of recruitment. For instance, cruises typically occur from early September to late October; if emigration of YOY from estuarine nursery grounds occurs after sampling in a given region, the abundance of spring-spawned individuals, in particular, may be underestimated.

### *Availability of Principal Prey in Relation to YOY Bluefish Recruitment and Habitat Use*

Variability in the timing of production of YOY bluefish and their prey among putative nursery habitats may explain differential patterns of habitat utilization at certain spatial scales. I found that the earliest-spawned individuals of the spring cohort almost exclusively recruited to estuarine (Chesapeake Bay) v. coastal ocean habitats, and that within estuarine habitats the spring cohort dominated in overall YOY abundance (Chapter 1). In contrast, although the spring cohort was present in coastal areas, the summer cohort dominated. These differences in macro-scale (ocean v. estuary) habitat utilization between YOY bluefish cohorts may, in part, be related to availability patterns of piscine prey between nursery habitats.

Based on prey availability, littoral habitats of Chesapeake Bay appear to be suitable nursery habitats for spring-spawned YOY bluefish, which begin appearing as early as mid-May, but typically occurred during the first week of June. Across all years, silversides, the dominant prey of YOY bluefish in littoral habitats, co-occurred with YOY bluefish on initial recruitment dates. Juanes and Conover (1995) also reported an early temporal match of peak abundances for spring cohort YOY bluefish and silverside prey across four years in Great South Bay, NY. Spawning of silversides occurs from April to June; small YOY (~30 mm) are generally abundant in MAB estuarine habitats by early June (Able and Fahay 1998). Prey types of lesser importance in littoral habitats of Chesapeake Bay were clupeids (e.g., *Alosa sp.*) and moronids (e.g., *Morone saxatilis*), which also exhibit peak spawning early in spring and whose YOY are most abundant during late spring when spring-spawned bluefish recruit to estuarine habitats. One might expect Chesapeake Bay to also be important for the summer cohort of YOY bluefish, because YOY bay anchovy abundances are very high in Chesapeake Bay during mid-August to early September. However, the summer cohort is rare in Chesapeake Bay (Chapter 1). This finding suggests that other factors (e.g., spawning geography, temperature, alternative suitable nursery grounds, etc.) may influence habitat utilization by this cohort.

Summer-spawned YOY bluefish were most prevalent in coastal ocean habitats, which appear to support an abundant bay anchovy forage base. Little is known about seasonal abundance and reproductive patterns of bay anchovy in coastal ocean environments, as this species generally is presumed to rely mostly on estuarine habitats for reproduction and growth; inner continental shelf environments are believed to serve primarily as a migratory corridor and overwintering grounds (Able and Fahay 1998). Unfortunately, our coastal sampling effort did not include early spring months (March – April), when bay anchovies re-enter near-shore nursery habitats from overwintering grounds. However, we did sample during fall (October – November), when bay anchovies typically emigrate from near-shore nursery habitats to the continental shelf. Thomas et al. (1974) compared bay anchovy catches from Great Bay-Mullica River Estuary, NJ to those in the adjacent coastal ocean (< 6.5 km from shore), and found relative abundance (CPUE) was: 1. similar between estuarine and coastal areas during spring (March – May); 2. higher in the estuary (CPUE = 71.8) than the ocean (CPUE = 25.0) during summer (June – August); and 3. again similar between habitats in fall (September – November). Vouglitois et al (1987) reported a similar trend, based on NMFS fall bottom trawl surveys in MAB shelf waters, where abundances on the shelf were highest and similar in spring and fall, and were lowest during summer. In 2001 and 2003, we sampled during June in Maryland coastal waters; bay anchovy were present in June, yet their relative abundance was significantly lower compared to later summer months (Table 2.14). These results suggest that bay anchovy routinely utilize shoal coastal ocean environments in addition to estuaries during summer months.

A resident "shelf" population of bay anchovy probably exists (E. Houde, personal communication), or some individuals may initially enter estuaries during spring and then migrate to the coastal ocean in summer. Interestingly, in Maryland coastal waters I observed high catches (mean CPUE = 239 $\pm$ 67.3 tow$^{-1}$) and occurrence (88%) of bay anchovy during the last week of May 2003, when water temperatures were fairly low (mean integrated water column temperature = 13 $^{o}$C). Yet only three weeks later, we observed low catches (3 $\pm$ 2.6 tow$^{-1}$) and occurrence (25%), when average water temperature was much higher, 20$^{o}$ C. These limited results provide support for a resident population of bay anchovy in the coastal ocean. For instance, if temperature induced movements from cooler coastal waters to warmer estuarine waters, then we would have expected higher, rather than lower abundances of anchovy at 20 v. 13 C (i.e., June v. May). Further, this pattern was observed in late spring, when anchovies are assumed to have already entered estuaries from offshore overwintering habitats. The lack of YOY bluefish in coastal environments in late spring is likely attributed to lower anchovy prey availability and temperature. Anchovy average sizes in June (75 mm in 2001; 73 mm in 2003) were likely too large for small, recruiting bluefish to consume. However, high abundances and small sizes of bay anchovy in the coastal ocean occur during late summer months (August – September), sustaining ample forage for the summer cohort of YOY bluefish.

Substantial spawning activity by bay anchovy probably occurs in coastal ocean environments. Sherman et al. (1984) reported larval abundances as high as 1,000 $m^{-2}$, but typically 11 – 100 $m^{-2}$, during summer (June – August) in inner margins of MAB shelf waters across four years of MARMAP surveys. Further, Milstein and Thomas (1977) found similar egg densities between estuarine (16.9 – 78.6 $m^{-3}$ in Great Bay estuary, NJ) and coastal ocean environments (11.7 – 58.3 $m^{-3}$, < 6 km offshore of Great Bay estuary) during June and July. Rilling and Houde (1999) reported highest larval densities in Chesapeake Bay also occurred from June – July: means for this period were 243 $m^{-2}$ (Bay-wide) and 695 $m^{-2}$ (Lower Bay). These results suggest that spawning of bay anchovy occurs in coastal ocean environments in addition to estuaries, generally peaking in July in both. Further, anchovy production may be on the same order of magnitude between habitats, given the similarity of larval and egg densities. Alternatively, it is possible that spawning in estuarine habitats may provide substantial ‘leakage’ of larvae/juveniles into coastal ocean habitats (E. Houde, personal communication). For instance, I observed similar interannual patterns of bay anchovy abundances between ocean and estuarine habitats (e.g., highest abundances in both habitats occurred in 2000, Fig. 2.23). However, Maryland coastal waters and the mouth of the Chesapeake Bay are separated by > 150 km and the south-flowing long-shore current would indicate little connectivity between the Chesapeake Bay and sampled coastal environments. Moreover, Sherman et al. (1984) did not observe higher egg and larval densities immediately adjacent to estuaries, which would have been expected, were coastal productions dependent upon estuaries. Finally, primary production levels reported for estuarine and coastal ocean habitats are similar. Sherman et al. (1984) reported mean annual primary production of 360 g C $m^{-2}yr^{-1}$ in inner shelf waters off the DelMarVa peninsula, while Harding et al. (2002) reported mean annual levels of 408 g C $m^{-2}yr^{-1}$ for Chesapeake Bay. These comparable primary production levels suggest that both systems can support high zooplankton stocks and associated YOY anchovy production.

I observed that YOY bluefish consistently selected for small bay anchovy (Fig. 2.21); this pattern has also been observed in a host of previous studies for bay anchovy, in addition to other piscine prey (e.g., silversides and striped bass) (Juanes et al. 1994; Juanes and Conover 1995; Scharf et al. 1998; Buckel et al. 1999a). I observed that YOY bluefish generally consumed bay anchovy prey of 30 – 50 mm (Fig. 2.21); larger YOY continued to consume relatively small bay anchovy, although maximum prey sizes consumed did increase with increasing bluefish size (Fig. 2.19). Average sizes of bay anchovy in the coastal ocean changed seasonally in 2003, with decreased average sizes among successive cruises (Table 2.9) indicative of a prey population dominated by mature adults in the spring and primarily YOY during summer and fall months. The fact that little overlap existed between trawl-collected and bluefish-consumed length distributions for bottom trawl collections (Fig. 2.21) suggests that the large bottom trawl (6.4 mm mesh in the cod end) we used may not efficiently capture early-juvenile stages (30 – 40 mm) of bay anchovy. Indeed, smaller bay anchovy (~ 40 mm TL) were common in mid-water trawl collections in Chesapeake Bay. Therefore, the bottom trawl does not appear to sample small YOY anchovy as effectively as the mid-water trawl; anchovy abundances based on bottom trawl data may be underestimates of actual abundances of YOY bay anchovy "available" to juvenile bluefish.

The high abundances of bay anchovy I observed in coastal ocean habitats, during periods when the summer-spawned bluefish were also abundant, supports my hypothesis that coastal ocean environments function as important nursery habitats for summer-spawned bluefish. Although bay anchovy abundances were significantly higher in channel habitats of Chesapeake Bay than Maryland coastal waters (Fig. 2.23), this does not necessarily imply that Chesapeake Bay is a superior nursery habitat for YOY bluefish in comparison to the coastal ocean. Firstly, YOY bluefish may primarily utilize littoral, rather than channel estuarine habitats. The interannual abundance trends I observed in mainstem Chesapeake Bay were inconsistent with those observed in littoral habitats (based upon seine monitoring by Maryland DNR). Secondly, differences in temporal aspects of sampling between systems (at both daily and seasonal temporal scales) could bias system comparisons of bay anchovy abundance. For instance, collections in Chesapeake Bay were made during night, and because bay anchovy exhibit diel vertical migration (upwards at night, tracing the migration of their primary prey, copepods, Vouglitois et al. 1987), they would be more susceptible to capture during night v. day using a pelagic gear (i.e., the mid-water trawl). A potential seasonal bias, perhaps less important than the aforementioned, is the effect of fall emigration of bay anchovy. Voiglitois et al (1987) found evidence (low catches in the estuary complemented by increased abundance in shelf waters) suggesting emigration from estuaries to the coastal ocean occurs sometime during October – November in New Jersey. However, in more southerly estuaries (i.e., south of Delaware), bay anchovy may primarily overwinter within estuaries rather than emigrating to the inner continental shelf. For instance, in Chesapeake Bay, bay anchovy are believed to primarily overwinter in the lower Bay, except during extremely cold winters (Wang and Houde 1995; Jung and Houde 2004). Therefore, trawl collections in the coastal ocean during fall (October – November) may include anchovy resident to the ocean in addition to emigrants from northerly estuaries (e.g., Delaware Bay); potentially, this may bias upwards relative abundance estimates in the coastal ocean. However, increased abundances were not observed in the ocean from September → October in 2003 or September → early November in 2004.

Abundance levels at which bay anchovy prey become limiting for juvenile bluefish in respective systems is likely a very important factor influencing recruitment success (to age 1+ stages) and nursery habitat suitability for juvenile bluefish. Bay anchovy is the most abundant fish in Chesapeake Bay, and likely are not limiting for juvenile bluefish. In coastal ocean environments, I observed possible evidence of prey limitation, whereby feeding incidence on anchovy was significantly lowest when (2003) lowest relative abundance levels also occurred. There was no positive association of mean annual abundance/occurrence of YOY bluefish with bay anchovy in the coastal ocean. In fact, the trend appeared to be negative. Lowest abundances of YOY bluefish occurred in 2000, when highest abundances of bay anchovy were observed; highest bluefish abundances occurred in 2001, when bay anchovy abundance was intermediate (Figs. 2.22, 2.23). Interestingly, Takata (2004) found that growth rates of YOY bluefish were very high in 2000 (2.63 mm $d^{-1}$) and rather low in 2001 (1.45 mm $d^{-1}$). These results indicate possible density-dependent influences on growth rates. In 2003, despite low anchovy abundances, YOY bluefish (at least the summer cohort) were fairly abundant. During this year, high dependence upon invertebrate prey by summer-spawned individuals may have contributed to a lower growth rate in 2003 (1.98 mm $d^{-1}$), than in 2000 (2.63 mm $d^{-1}$) and 2004 (2.40 mm $d^{-1}$) (Takata 2004; Chapter 1). The increased contribution of invertebrate prey could have potentially resulted in lower recruitment (to age1+) of summer-spawned bluefish produced in 2003 relative to other years, if they over-wintered at relatively small sizes and suffered higher mortality.

### *Conclusions and Future Work*

A chief criterion of nursery habitats for juvenile fishes is an adequate forage base (both abundance and size); this may be *the* most important factor influencing growth and survival of young-of-the-year bluefish, which are capable of complete piscivory upon recruitment and may not experience high predation mortality during the juvenile stage. My study shows that, by this criterion, coastal ocean environments function as vital nursery grounds for juvenile bluefish, especially summer-spawned individuals, which primarily rely on abundant YOY bay anchovy resources. Growth and survival of summer-spawned bluefish in coastal ocean nurseries is probably closely linked with population dynamics of bay anchovy, because it appears that suitable alternative piscine prey in the coastal ocean are rare in the MAB. Further, it is noteworthy that in 2003 summer-spawned bluefish continued to utilize coastal environments even when bay anchovy abundance was relatively low. Bay anchovy are also likely important in sustaining young bluefish during their fall southward migration and subsequent overwintering periods (Buckel et al. 1999a). As reported in previous studies, I found that littoral estuarine habitats possess abundant and diverse piscine prey resources, and afford suitable habitats for spring-spawned bluefish. Comparisons of competition intensity between coastal and estuarine habitats may provide further insight into spatiotemporal habitat use patterns for juvenile bluefish.

The foremost knowledge gap and potential future research avenue regarding bluefish foraging ecology is a better understanding of the population dynamics of bay anchovy in coastal ocean environments. For instance, we need a better understanding of population structure and size, seasonal abundance, and reproduction to understand linkages between prey production and bluefish production. Given this information, it should be possible to develop habitat suitability indices, based on bioenergetic models (supply, demand, etc.). Also, because high occurrence of invertebrate prey was observed in some years in the coastal ocean, stable isotope analysis could highlight foodweb dependencies and effects on growth rates of YOY bluefish. Finally, little is known regarding key predators of YOY bluefish in estuarine and coastal habitats, and this knowledge could provide valuable insight into biotic regulation of bluefish populations.

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